Eesti Maaülikool
Estonian University of Life Sciences

COASTAL MEADOWS: MAINTENANCE, RESTORATION AND RECOVERY

RANNANIIDUD: SÄILIMINE, TAASTAMINE JA TAASTUMINE

MARIKA KOSE

A Thesis
for applying for the degree of Doctor of Philosophy
in Agriculture

Väitekiri
filosoofiadoktori kraadi taotlemiseks
põllumajanduse erialal

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LIST OF ORIGINAL PUBLICATIONS

This thesis is a review of the following papers, which are referred to by Roman numerals in the text. The papers are reproduced by permission of the publishers.

I **Kose, M.**, Heinsoo, K., Kaljund, K., Tali, K. 2020. Twenty years of Baltic Boreal coastal meadow restoration: has it been long enough? Restoration Ecology.

II **Kose, M.**, Liira, J., Tali, K. 2019. Long-term effect of different management regimes on the survival and population structure of *Gladiolus imbricatus* in Estonian coastal meadows. Global Ecology and Conservation 20: e00761.

III Moora, M., **Kose, M.**, Jõgar, Ü. 2007. Optimal management of the rare *Gladiolus imbricatus* in Estonian coastal meadows indicated by its population structure. Applied Vegetation Science, 10, 161–168.

Table 1. Authors' contributions to the papers

Paper	Idea and study design	Laboratory and fieldwork	Data analysis	Manuscript preparation
I	**MK**, KT	**MK**, KK	KH, **MK**, KT	**MK**, KH, KK, KT
II	**MK**, JL, KT	**MK**	JL, **MK**	**MK**, JL, KT
III	MM, **MK**, ÜJ	MM, **MK**, ÜJ	MM, ÜJ, **MK**	MM, **MK**, ÜJ

JL – Jaan Liira; KK – Karin Kaljund; KH – Katrin Heinsoo; KT – Kadri Tali; **MK - Marika Kose**; MM – Mari Moora; ÜJ – Ülle Jõgar;

1. INTRODUCTION

Coastal grasslands around the Baltic Sea, called the Boreal Baltic coastal meadows, are seminatural plant communities of high conservation value and importance to the European Union. They need constant grazing and/or mowing management to sustain them and prevent natural succession. For the last two decades, their restoration and maintenance have been important conservational tasks in Estonia, Sweden, Finland and Latvia because changes in land use (mainly abandonment) have caused large-scale loss or degradation of coastal meadows.

Restoration activities have a few aims: to gain more grassland area; to enlarge and connect fragmented habitats; and to benefit target species, like *Bufo calamita*, *Coeloglossum viride*, waders and migratory birds. Less attention has been paid to the recovery of plant communities and their habitats. As management activities have to comply with the European Union Common Agricultural Policy and agri-environmental scheme, the metrics to assess the results are simple. Vegetation quality is measured by the height of vegetation and *Phragmites australis*, and the proportion of low-sward grass. Conservation authorities carry out the monitoring of target species to evaluate their recovery. While species' richness and composition are common measures to evaluate the success of restoration activities, it is difficult to evaluate the quality or recovery of coastal meadows in this way. There are numerous plant communities with great diversity, and it is difficult to identify indicator species that are present in all coastal meadows.

Current thesis was motivated in 2013 by the complex national policy for coastal meadow management and by the gaps between real-life situations and legislative documents. We discuss conservation and agricultural policies that promote restoration and management of seminatural grasslands, examining their applicability to real situations in the field. To better understand the reasons why current policy tools have had a limited positive impact, we assess the success of restoration and recovery efforts targeting the vegetation of coastal meadows in Estonia. We describe the specific traits of vegetation that can be used to assess the habitat quality of coastal meadows. We also discuss the timescale of vegetation recovery, providing examples of short- and long-term restoration activities' impacts on protected plant species.

2. REVIEW OF THE LITERATURE

2.1 Coastal grasslands as semi-natural communities

Semi-natural communities are relatively stable ecological communities with native species that spontaneously established They develop over a long period of time as a result of moderate human activity, mainly grazing and haymaking. Although they have no trace of ploughing, fertilising or artificial seeding, semi-natural ecosystems are permanent grasslands. Certain types of human agricultural interference are needed; in European latitudes, cessation of such activities leads to scrub and tree encroachment, and the grassland disappears (Eriksson et al., 2002; Pärtel et al., 2007).

The Baltic Sea coast constitutes an important part of Europe's diverse landscape (Dijkema 1990). Under natural conditions, littoral grasslands occur only at a small scale and/or temporarily exist on newly formed terrain. As they have been extended through mowing and grazing over hundreds of years, large-scale, resilient and persistent coastal grasslands occur along almost the entire Baltic Sea coast (Pätsch et al., 2019). Because human activities have shaped them, they are regarded as semi-natural communities (Eriksson et al., 2002; Pärtel et al., 2007).

Coastal meadows are categorised as European Union (EU) habitat types H1330 (Atlantic salt meadows) and H1630 (Boreal Baltic coastal meadows). The latter is rated as a priority in Annex I of the EU Habitats Directive (European Commission, 2013). Additionally, Boreal Baltic coastal meadows are considered to be endangered on the European Red List of Habitats due to their rapid decline in the second half of the twentieth century. Today, they are among the most threatened habitats in Europe (Joyce, 2014; Lotman and Lepik, 2004; Rannap et al., 2017). Our thesis describes the restoration of these habitats after their abandonment from the late 1940s until 2000. Restoration activities can adopt a pre-abandonment focus (Valkó et al., 2016) and try to restore habitats to their original state, but this is complicated for most habitats today because of the changes in the environment. The maintenance of semi-natural grasslands, including coastal meadows, is considered to be one of the most important tasks in Estonia's nature conservation strategy (Keskkonnaministeerium, 2012). The degradation of coastal grasslands, which was caused by land abandonment and subsequent reed (*P. australis*) encroachment, is typical situation in the Baltic Sea region. In Estonia, the largest area of coastal meadows under management (about 35 000 ha) was reported in 1900. During the 20th century, this area gradually reduced; in the 1960s, it was 29 000 ha, and in 1981, it was 9 500 ha. By 2000, the area of managed coastal meadows had decreased to 5 100 ha (Luhamaa et al., 2001).

2.2 Grassland restoration and recovery

Coastal meadows' high conservation value, ecosystem services and species richness have motivated restoration and management activities in the last few decades (Wanner, 2009; Sammul et al., 2012, Valko et al., 2018). The first attempts to restore coastal meadows in Estonia took place in 1997 in Matsalu National Park (Lotman et al., 2014). Since then, restoration and management activities have increased slowly but steadily. By the end of 2020, 12 423 ha of coastal meadows were managed under an EU agri-environmental scheme, and 979 ha were the target of ongoing restoration activities (Keskkonnaamet, 2021). The managed area includes about 5 100 ha that have been constantly managed for centuries and 7 323 ha that have been restored from abandonment since 2000.

The main restoration measures that are applicable to coastal meadows in Estonia are described in detail by Lotman and Lepik (2004) and revised in the Estonian coastal meadows' management plan (Lotman and Rannap, 2020). Although historically the meadows were used as pastures for all domestic animals—and, in some cases, for haymaking—nowadays, beef cattle are preferred for restoration and habitat management purposes (Kasvandik et al., 2003; Sammul et al., 2012; Laurila et al., 2015). Coastal meadows in favourable conservation status have no trees or shrubs, only low vegetation, due to grazing or mowing.

Kose et al. (2019) have described various management patterns with different animals and mowing strategies **(II)**. One common restoration practice is to actively destroy reed and remove shrubs from meadows by mowing (machine cutting with removal of biomass, typically hay) or mulching (machine cutting or crushing without biomass removal). This enables the reintroduction of grazing as soon as possible and, by improving light conditions, encourages the establishment and spreading of coastal grassland-specific plant species. Typically, it takes two to three years to clean meadows of shrubs and dead reed and to suppress reed growth to an extent that allows for grazing.

Once these conditions are fulfilled, the area can enter the EU agri-environmental scheme for semi-natural habitat management. In total, 7 323 ha of coastal meadows that have undergone this short restoration process qualify as "managed meadows," rather than "restored" or "under restoration." The evaluation criteria for entering the agri-environmental scheme are the proportion of short vegetation (more than 50% of the area) and the height of reed in the late summer (less than 50 cm). Corrective mowing or mulching in the late summer may be needed in the first five years to suppress reed and meet the criteria (Lotman and Rannap, 2020).

To date, the main targets of coastal meadow restoration have been endangered bird and amphibian species (Hellström and Berg, 2001; Rannap et al., 2007; Durant et al., 2008; Zmihorski et al., 2016). However, many papers note that neither restoration nor conservational management has achieved the desired results in terms of restored area, quality or recolonisation of coastal meadow bird and amphibian species (Raatikainen et al., 2017; Rannap et al., 2017, Holm et al., 2019). Other studies have indicated the need for more measurable goals related to vegetation recovery (Bakker et al., 2000; Gustavsson et al., 2011; Walden and Lindborg, 2016; Török and Helm, 2017). As it is presumed that endangered bird and amphibian species recolonise meadows after vegetation functionality has recovered, it is reasonable to evaluate the speed and course of restoration based on the characteristics of plant communities (Baur, 2014).

Plant species composition and richness have been used as the main indicators in evaluations of grassland management and restoration (Baur, 2014; Horrocks et al., 2016; Walden and Lindborg, 2016), although some have used different indicators (Öckinger et al., 2006). It is well known that grazing increases species richness by reducing the competition for light and providing growth opportunities to small species. In the absence of management, grassland communities experience a decline in the species richness of vascular plants (e.g. Rosen, 1982; Wehn et al., 2018; Kapas et al., 2020) and abandonment gives way to successional changes. In coastal grasslands, the first phase of abandonment involves overgrowth by reed.

Species richness, or number of species, is generally considered to be the simplest metric to represent diversity, and it is the most commonly applied. Typically, coastal meadows do not show very high plant small scale species diversity; their species pool is 28 to 53 (Pärtel et al., 2007, Wanner, 2009). Lower values than that usually reflect a high proportion of reed (or other tall grasses). A coastal meadow with good conservation status should exhibit high evenness in terms of species distribution (e.g. Berg et al., 2012).

Some authors have shown that concentrating on fixed species makes it more difficult to compare sites and regions and have suggested that studying functional characteristics of plants could be a solution (Kahmen and Poschlod, 2008; Török and Helm, 2017). Some functional characteristics relate to management (Bullock et al., 2001; Kahmen and Poschlod, 2008; Wellstein et al., 2011; Koch et al., 2017). One example is plant height, which is usually considered to be a surrogate for competitive ability (Violle et al., 2007). Adult plant height is the most common measure of whole plant size, and it indicates a plant's ability to pre-empt resources and outcompete other species (Díaz et al., 2015). Plant height also reflects grazing tolerance, a short lifespan and stoloniferous and rosette growth (Diaz et al., 2004). The coverage ratio of high- and low-growing plants should indicate how long and how effectively a coastal meadow has been managed, as a species-rich coastal meadow mostly consists of low-growing plant species. Ellenberg species indicator values (EIVs; Ellenberg et al., 1991) are often used to better understand and describe abiotic conditions at sampling locations in grasslands (Kladivová and Münzbergová, 2016; Hülber et al., 2017; Benthien et al., 2018). The EIV values – salt tolerance (S), humidity tolerance (F), and light demand (L) – are specific to coastal meadows.

Recovery time is a topic of debate. Sammul et al. (2012) indicated that after five years of restoration, some desired or typical species had returned to the coastal meadow research areas. However, the height of vegetation and cover of common reed was not suppressed. Additionally, there were delays in restoration success in wetter and more nutrient-rich areas, indicating site-specificity. During a five-year experiment, Berg et al. (2012) reported an increase in bare ground during the first few years of coastal meadow restoration due to mowing and only small changes in vegetation.

Some positive impacts on species diversity in grasslands have been reported after 5 to 10 years of management. For example, positive impacts were reported by Bakker et al. (2003) for natural and artificial salt marshes in the Wadden Sea area; by Lindborg and Eriksson (2004) for Swedish seminatural grasslands; by Kose et al. (2019) **(II)** for Estonian coastal meadows; and by Lundberg et al. (2017) for coastal dune meadows in Norway.

Other authors mention that long periods of time are needed for restoration, but they do not indicate whether these periods are years, decades or centuries in length (Török and Helm 2017). However, they do suggest that the longer the period of abandonment, the longer, more challenging, expensive and time-consuming the restoration process will be (Valkó et al., 2018).

2.3 Target and non-target species

The main targets of coastal meadow restoration are endangered bird and amphibian species included in the European Union Habitats and Birds Directives (Hellström and Berg, 2001; Rannap et al., 2007; Durant et al., 2008; Zmihorski et al., 2016). The coastal meadow restoration activities from 2001 to 2005 in the Luitemaa Nature Reserve, one of our study sites, were not focused on maintaining the *Gladiolus imbricatus* (sword lily) population, but on creating a habitat for rare shorebirds (Kose et al., 2004).

G. imbricatus (*Iridaceae*) is a decorative tuberous clonal plant (Figures 1 and 2) that is native to Central and Eastern Europe, the Mediterranean, Caucasia and West Siberia (Meusel et al., 1965). *G. imbricatus* can reach 30–100 cm tall. It forms bulb-like tubers that are 1–2 cm in length and tubercles for vegetative reproduction. Vegetative plants start as single-leaf juveniles and then grow to become two-leaved premature plants. Generative plants have single slender stalks with two rosette leaves, one to three leaves on the flower stalk and three to ten purple flowers within a one-sided inflorescence. In Estonia, flowering occurs in July, and relatively large seeds (1.8 mg) ripen during the first half of August. One plant can produce 200–400 seeds, and a chilling period of several months is needed for the seeds to germinate when temperatures increase in late spring (Rakosy-Tican et al., 2012).

Figure 1. *Gladiolus imbricatus* on a mown part of a coastal meadow in Ruskiranna, Pulgoja, on 7 July 2014 (photo: Märt Kose).

Figure 2. Flowering stalks of *G. imbricatus* in a mown meadow in Ruskiranna, Pulgoja, on 7 July 2014 (photo: Märt Kose).

From 2001 to 2002, the restoration site was visited by Sabine Hänel, a German botanist, who studied *G. imbricatus* and its populations. We were inspired by her work to expand the scope of restoration, which was too narrow, and focus on the whole range of ecosystem services and biodiversity issues rather than very specific target species. There are around 30 plant species residing in coastal grasslands that are protected at the national level, such as orchids (*Dactylorhiza baltica*, *D. incarnata*, *Platanthera bifolia* and *Coeloglossum viride*) and grasses and sedges (*Carex glareosa*, *C. mackenziei*, *C. extensa* and *Schoenus nigricans*). Aside from some common orchids, these species were not present in our research area. We consider *G. imbricatus*, a tall perennial herb, to be a good flagship species to study a very important side effect of the grassland restoration process: the response of a rare grassland species to various types of maintenance. *G imbricatus* is decorative, noticeable and relatively abundant in grasslands under all management regimes at the start of restoration activities.

The *G. imbricatus* species is categorised as threatened, red-listed or protected across Europe (Kostrakiewicz-Gieralt et al., 2018), and it has become locally extinct in numerous regions (Richter, 2012). In Estonia, *G. imbricatus* is under legal protection and is considered to be vulnerable (Kull et al., 2018), as its population is in decline (Kukk and Kull, 2005). *G. imbricatus* occurs in a range of habitats across Europe, from thermophilus oak forests to wet meadows, including floodplains, coastal grasslands and marshes (Kostrakiewicz-Gieralt, 2014b; Kostrakiewicz-Gieralt et al., 2018). In Estonia, its species distribution is restricted to a sub-region of Livland (the southern half of the country), forming a west–east belt from coastal meadows in the west to flooded meadows near the River Emajõgi in the east (Kukk and Kull, 2005). The species is threatened by the picking of flowering plants and changes in land use (i.e. abandonment and urbanisation of coastal areas). During the previous century, abandonment of the seashore and floodplain grasslands resulted in the encroachment of reed and bushes. Grazing, which is the most traditional measure of grassland restoration, is unadvisable for the species (Krall et al., 2010; Richter, 2012). Reintroduction has been recommended in locations where the species has disappeared (Jõgar and Moora, 2008).

2.4 Policies, measures and resources securing semi-natural grassland management

Due to the high value of conservation at the Estonian and European scales, several measures have been taken and resources have been allocated for the restoration and ongoing management of coastal meadows. The main policy in the EU is the Common Agricultural Policy, which includes an agri-environmental scheme with horizontal instruments and direct payments from Pillar 1 and EFARD payments from Pillar 2 (Alliance Environnement, 2019). In EU member states, like Estonia, national funds can be allocated and additional policies can be implemented to target biodiversity aims in semi-natural grasslands (Holm et al., 2019).

Alliance Environnement's (2019) final report, titled 'Evaluation of the Impact of the Common Agricultural Policy on Habitats, Landscapes, Biodiversity', concludes that on the basis of the available evidence, some of the Common Agricultural Policy instruments and measures are making significant contributions to conservation and, to a lesser extent, restoration of semi-natural farmland habitats and their species, which are of particularly high biodiversity importance. The report also concludes that, due to a lack of data, it is not possible to estimate the net combined impact of the Common Agricultural Policy instruments and measures on biodiversity, even in semi-quantitative terms. However, overall, biodiversity monitoring evidence indicates that the combined effects of the Common Agricultural Policy have not been sufficient to counteract the pressures on biodiversity from agriculture in both semi-natural habitats and more intensively managed farmland. The same criticism of the Common Agricultural Policy and its measures can be found in the work of Pe'er et al. (2014), Pe'er et al. (2017), Concepcion et al. (2020), Pardo et al. (2020) and Ravetto et al. (2020).

In Estonia, Holm et al. (2019) performed a thorough analysis published as 'Securing the Sustainability of Semi-natural Grasslands Management'. The report's findings align with European analyses, finding that, in spite of all efforts, there are problems associated with restoring semi-natural grasslands, including coastal grasslands. Funds from the EU agri-environmental scheme are not used for restoration activities in Estonia, although such activities would be eligible for Member States. All EU funds are used only on Natura 2000 areas, even though they could also be used elsewhere. There are 13 800 ha of coastal meadows in protected areas, and the overall potential is 20 478 ha (Holm et al., 2019). Also, EU funds could be used to target nationally protected biodiversity objects in semi-natural grasslands. However, in Estonia, the funds are not widely used, especially for plant species, very few of which are listed in Annex II of the EU Habitats Directive. Another problem emerging from national implementation of EU funds is that the evaluation of activities – and, therefore, the basis of payment – is based on the activities themselves, not their created value. Activity-based assessment (i.e. whether mowing or grazing is present or not on a certain number of hectares) does not reflect the activities' impact on biodiversity. In some other countries, such as Finland and Sweden, the value of activities is integrated into the payment scheme (Holm et al., 2019).

The research and policy gaps revealed by literature and practical experience motivated the research described in this thesis. Throughout the research and publication process, the results and recommendations have been – and hopefully will continue to be – considered in Estonian restoration practices and legislative documents.

3. THE HYPOTHESIS AND AIMS OF THE STUDY

This work investigated the timescale of recovery and criteria for assessing the recovery of coastal meadow vegetation (**I**) and studied the response of a non-target species, *G. imbricatus*, to restoration activities in the short- and long-term scale in order to determine whether all restoration and management measures suit rare plant species (**II** and **III**). The legal framework for semi-natural communities and the EU Common Agricultural Policy are not sufficient to support achieving the biodiversity targets of coastal meadows. There is a need to consider vegetation restoration and recovery processes in a more complex way to support not only plant species but also overall biodiversity (**I**, **II** and **III**).

The objectives of this work are as follows:

1. To establish a temporal scale for coastal meadow restoration, determining how long it takes for coastal meadow vegetation to be restored and how to assess success in the context of restoration. (**I)**
   H1: Coastal meadow vegetation recovery is related to the time of abandonment.
   H2: Permanently managed meadows are good references for coastal meadow recovery.

2. To study short- and long-term restoration activities and assess their impact on population level, using the example of *Gladiolus imbricatus*, as a protected but non-target species for restoration. (**II** and **III**)
   H3: Restoration activities have a rapid positive impact on population growth under all management types (mowing, grazing with sheep and cattle).
   H4: Different management practices vary in their impact on long-term recovery and the persistence of species restoration.

3. Based on our own work and prior literature, we aim to determine how the legal framework for semi-natural communities and the EU Common Agricultural Policy could better support the biodiversity targets of coastal meadows. (**I, II** and **III**)

4. MATERIAL AND METHODS

4.1 Field data collection

In 2005, Sammul et al. (2012) selected fourteen different coastal grasslands in four regions along the western coast of Estonia (Figure 1, **I**) based on information about their management history. Their research is summarised below:

> In each region, continuously managed, abandoned (neither grazed nor mown for 30 years before 2005) and restored (3–5 years before 2005) coastal grassland sites were selected as close to each other as possible to minimise the effect of site specificity on soils. Restored sites were selected as close as possible to abandoned sites (in Haeska and Piirumi, they were separated only by a fence between the pastures) in order to ensure similarity of vegetation and management history prior to the start of restoration. Managed sites were selected to have as similar geomorphology as possible to the abandoned sites. There were no recently restored sites available in Silma.
>
> All studied grasslands were relatively large and wide, and for most, the distance from the shoreline to the landward edge of the grassland exceeded 500 m. A relatively homogenous upper part of the saline zone was selected for study at all sites. Special care was taken to select areas without a clearly detectable elevation gradient in order to minimise differences in the salinity, effects of waves, sedimentation and so on between plots and to ensure compatibility between sites.
>
> At each site, 20 0.5 m x 0.5 m plots were investigated on two 90-m-long transects (ten plots per transect, 10 m apart) located 30 m from each other and perpendicular to the coastline. In each plot, the plant species composition was determined, the cover of each species was estimated and the vegetation height was measured. (Sammul et al., 2012)

The sites were revisited in 2015 (Figures 3, 4, 5 and 6), and sampling was carried out with the same methodology (**I**). This involved registering all vascular plant species in the plot, their coverage, total coverage and the maximum and median heights of vegetation. In 2015, all coastal meadow sites were managed by mowing or grazing under the EU agri-environmental scheme.

Figure 3. The Kastna study area in late July 2015. Restoration activities (grazing with beef cattle) began in 2010 (photo: Karin Kaljund).

From 2002 to 2004 and 2014 to 2016, a population study of *G. imbricatus* was carried out in coastal meadows in the Luitemaa Nature Reserve (southwest Estonia) with four different management regimes (grazing with cattle and sheep, mowing and abandonment) (Figure 1, **II**). In this reserve, meadow restoration began in 2001. The sites are near the sites of Häädemeeste and Piirumi I, which are described in (**I**). In 2002, two 20 x 20 m subsites were randomly selected at each site. Ten 1 m^2 plots were randomly selected at these sub-sites each year. Within these plots, *G. imbricatus* specimens were counted at three ontogenetic (life) stages: (1) juveniles (i.e. one-leaved seedlings and vegetative juveniles (Figure 3, **II**), (2) premature plants (i.e. two-leaved or vegetative adults) and (3) generative (i.e. flowering) plants.

Figure 4. Haeska 2 meadow in September 2014. Restoration began in 2001 with mulching and grazing with beef cattle (photo: Karin Kauer).

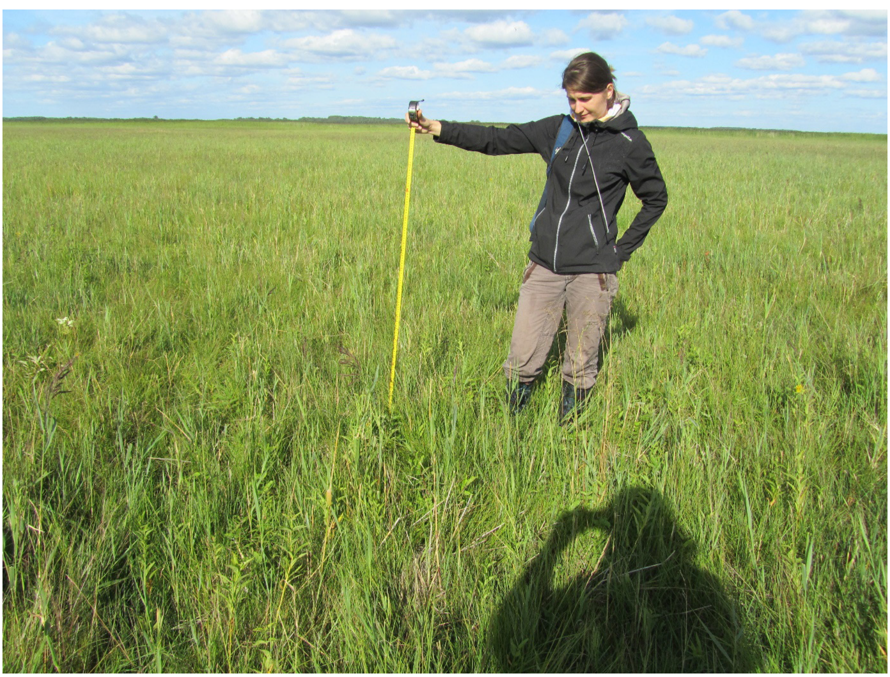

Figure 5. The Pürksi meadow in July 2015. Restoration began in 2006 with mulching and grazing with beef cattle (photo: Marika Kose).

Figure 6. The Põgari–Sassi coastal meadow in Matsalu National Park is considered to be one of the best coastal meadows in Estonia by conservationists (photo: Karin Kaljund, late July 2015).

The plant coverage, species composition (i.e. presence and cover), maximum height and upper height limit of leaves were reported for each plot. In 2016, another study was carried out to measure additional parameters (plant height, leaf number and height, flowering stalk height, number of flowers) of *G. imbricatus* specimens for comparison with the measured vegetation parameters (Figure 5, **II**). In 2019, juvenile and premature plants were excavated from each management regime (grazing by sheep and cattle, mowing and abandonment) to estimate the potential age of plants according to the morphology of bulbs/tubers (Figure A4, Table A.3, **II**). All one-leaved *G. imbricatus* specimens were regarded as juveniles, even though they were different ages (Figure 3, **II**). The proportion of juveniles at each bulb stage was similar in all treatments (Figure A4, Table A.3, **II**). We conducted an extra experiment (B) to assess plots at sites that were previously grazed by sheep and later mown.

4.2 Data management and statistical analysis

A general linear model (GLM) and principal component analysis (PCA) were used to analyse the 14 coastal meadow sites (**I**). Factors included the average EIVs for light availability (L), salinity (S), humidity (F) and water plants (F10) as well as the percentages of different life forms in the plots, such as hemicryptophytes (H), chamaephytes (C) (Raunkiær, 1934) and wintergreen plants (mainly grasses and sedges, which form a permanent grass mat). Salt tolerance was indicated by two categories: moderately salt-tolerant plants (EIV 4–5) and salt-tolerant plants (EIV 7–9). No species with an EIV of 6 were present in the meadows. We used the theoretical vegetation height (Krall, et al. 2010) to identify low-lying plants (those with a theoretical average height up to 25 cm) and medium-height plants (those with a theoretical average height of 26–50 cm). In addition, we measured the height of vegetation. We also included Shannon indices and the coverage of *P. australis* as factors in the analysis.

For data processing, we used SAS 9.4 software (SAS Institute Inc., Cary, NC, USA). Correlations between the variables were analysed with the SAS GLM. We analysed the impact of the management group (permanently managed, restored before or after 2005) on different plant community characteristics in 2005 and 2015. In our analysis, the species pool was based on the number of species counted in the measured plots (for values, see Table S1) (**I**). Analysis was performed with an analysis of variance (ANOVA) multiple-analysis tool (n = 259) as well as a Ryan-Einot-Gabriel-Welsch (REGW) post-hoc test. We considered the data from each plot to be independent observations and status to be a fixed factor with three levels (permanently managed, restored before or after 2005). The dynamics of community characteristics were studied with covariation analysis (community characteristic*year), and statistically significant differences were detected with a least-squares means test. In the multivariate dataset, the development of each site from 2005 to 2015 was visualised with PCA of the SAS PRINCOMP procedure. The R IndVal package (Dufrêne–Legendre indicator species analysis) was used to identify the indicator plant species for each management group (permanently managed, restored before or after 2005) (Dufrêne and Legendre, 1997).

For the population study of *G. imbricatus* in the first phase of restoration, statistical analysis was carried out with the Statistica 6.0 software package

(Anonymous, 2001) (**III**). ANOVA was used to analyse the number of individuals (total, juvenile, vegetative, generative) of *G.imbricatus* and the relative number of grazed individuals (grazed individuals/total individuals, hereafter referred to as the grazing proportion). Variables were log-transformed to meet the assumptions of the analysis. The Tukey HSD post-hoc multiple comparison test was applied to estimate differences between the treatments. In Paper **II**, plot-level data were pooled at the sub-site level, as sampling plots were located randomly within the sub-site each year. The effect of treatments, successive years, life stages and their interactions were evaluated based on the log-transformed count of individuals and a general linear mixed model. In the model, sub-plots were defined as random factors. The post-hoc pair-wise differences among specific management regimes were estimated using the Tukey HSD multiple comparison test. Another analogously structured model was run using logit-transformed frequency data regarding the life stages of specimens in various plots within a sub-site. The SAS 9.3 MIXED procedure was used for both analyses (SAS Institute Inc.) (**II**).

5. RESULTS

5.1 Restoration effects on vegetation parameters

The vegetation parameters and changes over 10 years of restoration activities and management (Table 1) (**I**) reveal that, in 2005, the number of species per plot in abandoned meadows was significantly lower (7.8) than in meadows that were restored before 2005 (10.2) or permanently managed meadows (9.2). Over 5 to 10 years of restoration between 2005 and 2015, the number of species per plot was adjusted, and there was no significant difference between management groups.

The same pattern was observed with evenness (Shannon E index); the average number of species per m^2 increased in most meadows but slightly declined in permanently managed meadows (Figure 2, **I**). This result could be explained by the different management histories of the meadows (Figure S1, **I**); meadows that were historically mown had a significantly higher number of species. The Shannon E index almost reached its maximum level by 2015 in meadows that had been restored both before and after 2005 (Figure S2, **I**). The Shannon E values for permanent meadows were similar in 2005 and 2015. The values for both groups of restored meadows became closer to those of permanent meadows by 2015, but they were still similar to the 2005 results for meadows restored before 2005.

The change in plant coverage over 10 years (Figure S3, **I**) differed between different management groups. For permanently managed meadows, coverage increased to 60–70%. Areas with recent restoration activities in 2005 and 2015 had coverage of less than 60%. All the meadows where restoration activities started after 2005 were reedbeds. Meadows restored before 2005 had recovered from active intervention over 10 years of management and reached coverage of over 60%. The average and maximum vegetation heights increased in permanently managed meadows and meadows that had been restored before 2005, but decreased in meadows restored after 2005 (Figure S4, **I**).

Table 1. The average values of the studied factors, grouped by management status, in 2005 (n = 120, 60, and 100 plots per group for groups permanently managed, restored before and after 2005, respectively). Significant differences were revealed by REGWQ tests in particular year by management regimes. Statistically significant differences were marked with various shades of gray, while the darkest indicating the highest value. All ratios are calculated plotwise, based on coverage.

a	ab	b	c

Year	2005			2015		
Management group	Permanently managed	Restored before 2005	Abandoned, Restored after 2005	Permanently managed	Restored before 2005	Restored after 2005
Number of species per plot (average)	10.2	9.2	7.8	9.8	9.3	8.8
Shannon H	1.78	1.56	1.35	1.75	1.61	1.56
Shannon E	0.8	0.72	0.67	0.79	0.74	0.76
Average plant coverage (%)	63	57	72	68	61	56
Average height of vegetation (cm)	16	19	106	22	32	45
Maximum height of vegetation (cm)	36	52	161	48	67	87
Coverage of low-lying plants (theoretical height up to 25 cm) from overall species pool	25.12	16.49	0.8	23.03	19.75	17.37
Ratio of low-lying plants (theoretical height up to 25 cm)	0.5	0.1	0.08	0.27	0.11	0.1
Ratio of medium-height plants (theoretical height 26–50 cm)	0.42	0.58	0.24	0.55	0.51	0.39
P. australis coverage (%)	< 1	7	30	< 1	10	20
Ratio of light-demanding plants	0.68	0.65	0.35	0.6	0.58	0.54
Ratio of humidity-tolerant plants	0.46	0.72	0.38	0.57	0.62	0.46
Ratio of moderately salt-tolerant plants	0.02	0.06	0.02	0.07	0.05	0.01
Ratio of salt-tolerant plants	0.46	0.01	0.09	0.22	0.13	0.08
Ratio of hemicryptophytes and cryptophytes	0.64	0.62	0.41	0.64	0.61	0.46
Ratio of wintergreen plants	0.8	0.65	0.57	0.66	0.61	0.54

The coverage of medium-height plants increased in permanent meadows and meadows restored after 2005, but decreased in meadows restored before 2005.

IndVal analysis revealed that nine plant species occurred only in permanently managed meadows in both 2005 and 2015 (Table 2, **I**). According to IndVal, altogether, 13 species served as indicators of meadows that were visually estimated as in favourable condition. Among these, eight species were found in permanently managed meadows in both 2005 and 2015, and four were found in permanently managed meadows only in 2015. Meadows restored before 2005 did not show such homogeneity (Table S2, **I**), but meadows restored after 2005 as well as those estimated as extremely poor included *P. australis* and *Atriplex calotheca* as indicators in both years (Table S2, **I**).

The coverage of *P. australis* had a significant influence on most vegetation parameters (Table 3, **I**). Its disappearance led to the appearance of plants with high light requirements (Figure S5, **I**), water tolerance (Figures S6A and S6B, **I**) and salt tolerance (Figures S7A and S7B, **I**). The only factor that did not depend on *P. australis* coverage was average plant coverage, as *P. australis* is part of plant coverage, and where it is present, coverage is higher.

5.2 Recovery time and indicators

The PCA graph shown in Figure 7 (**I**) graphically illustrates the qualities used to measure recovery of coastal meadow plant communities. The first PCA axis describes 44.91% of the relation between the qualities of favourable and poor meadows. The Shannon E index, light-demanding plant coverage and Shannon H index (indicating good quality) are on the positive end, while the average and maximum height of vegetation and coverage of *P. australis* are on the negative end. The second PCA axis describes 21.01% of the qualities on the positive end, like coverage, species pool and number of species, and those on the negative end, like coverage of wintergreen plants and moderately salt-tolerant plants.

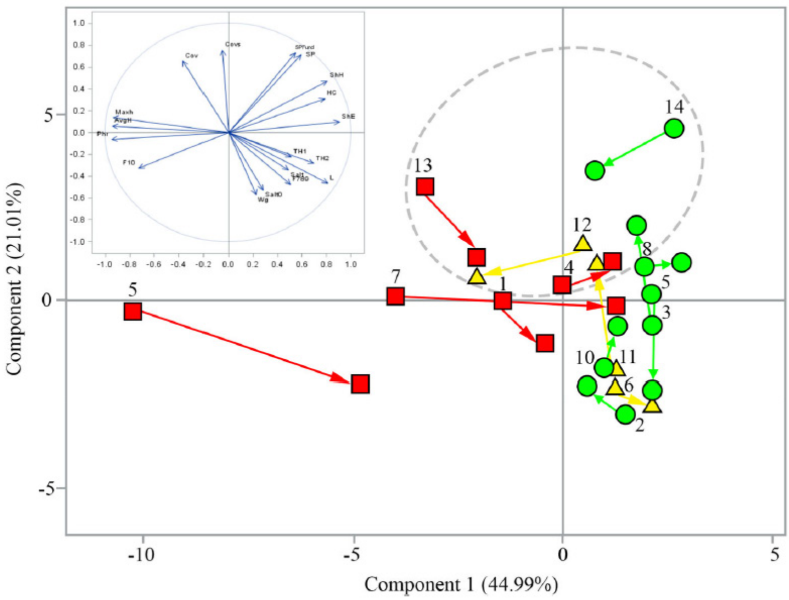

Figure 7. Dynamics of site development according to PCA (A) with a component pattern (B) by area from 2005 to 2015. Green dots indicate permanently managed meadows, yellow dots indicate meadows restored before 2005 and red dots indicate meadows restored after 2005. The closed circle with a dotted line indicates which meadows were historically mown. (**III**)

The results indicate that most of the meadows restored after 2005 have not reached the crucial qualities of good meadows that have been permanently managed or restored for a longer period.

5.3 Short- and long-term restoration effects on non-target species

5.3.1 Population size and structure

When restoration of coastal meadows began in late 2001 or early 2002, measurement for *G. imbricatus* also began. The mixed model results show very complex dynamics in terms of population size (Table 1, **II**). Analysis of the population structure for the first restoration phase (2002–2004) showed that experimental management treatments (grazing by cattle and sheep and mowing) changed the structure in different ways during the experiment ($\chi2 = 3272.7$, $P < 0.001$, $df = 14$) (Table 1, **III**). In the control (abandoned meadow), the population structure remained unchanged, while all manipulated populations responded to management. Mowing treatment resulted in a significantly higher proportion of juvenile plants and a lower proportion of generative plants than anticipated by the null model (Table 1). In both grazing treatments, the proportion of generative plants was significantly lower than that anticipated by the null model (Table 1, **III**).

The number of *G. imbricatus* juveniles increased during the first restoration phase (2002–2004) of the project for all treatments, particularly in mown plots (Figure 4A, **II**; Table 2 and Figure 2A, **III**). The abundance of juveniles in mown areas remained relatively high in the long term, even though the numbers reported from 2014 to 2016 were slightly lower than the peak observed in the third year of the experiment (Figure 2A, **III**). For the grazing treatments, however, after 10 years, the number of juveniles declined to the starting level of the 2002–2004 period or below. The initial increase was evident for juveniles in all treatments except for sheep grazing (Figure 2A, **III**). This was the case for long-term observations (**II**) in unmanaged areas in 2015 and sheep management plots in 2016 (Figure 4A, **II**).

The abundance of vegetative and generative shoots did not significantly vary between the treatments during the first two years of restoration (i.e. 2002 and 2003; Figure 4B–C, **II**). However, in 2004, the number of premature shoots declined in grazed plots and differed significantly from the estimates in mown areas. Detailed analysis of only data from the first year (Table 2, Figure 2B, **III**) showed differences between experimental treatments. The number of vegetative individuals did not change in the abandoned plots, increased in the mowing treatment, decreased significantly in the sheep pasture and marginally non-significantly ($P = 0.08$, Tukey HSD test) decreased in the cattle pasture. While analysing all data from 2002 to 2016, the numbers of premature and generative specimens were not statistically different from the numbers in the starting year across treatments, even though they decreased under both grazing treatments. The unmanaged plots showed the most stable populations of premature and generative specimens in the long term.

The number of generative individuals decreased during the experiment (Table 2, Figure 2C, **III**). The generative reproduction in the sheep-managed pasture was very poor (Figures 4 and 5, **II**), as all the shoots were bitten and none had flowers or fruits (Table A.4, Figure A5, **II**). During the first three years of the experiment, both grazing treatments significantly decreased the number of generative individuals (Figure 2C, **III**), and the number of generative individuals did not change for the abandonment and mowing treatments. Analysis of all data from 2002 to 2016 showed that the mowing treatment produced meadows with a significantly higher number of flowering specimens (Figure 4, **II**).

From 2002 to 2004, we investigated a former sheep pasture that was mown in 2003 and 2004. The proportion of juvenile plants was significantly higher for that treatment, and the proportions of vegetative and generative plants were lower than anticipated by the null model (Table 1, **III**).

5.3.2 The impact of sheep and cattle grazing

One of the research tasks was to estimate the effects of grazing by different livestock on the population structure of *G. imbricatus*. As data from the first period of restoration (2002–2004) were analysed separately (**III**) from data collected in the second period (**II**), the results are reported in different ways.

There were significantly more (Table 2, **III**) browsed individuals in the sheep pasture than in the cattle pasture (47 % and 28 %, respectively) in the first period. There was no difference in the second period according to an overall estimation (Table A.4, **II**), but there were differences between life stages (Figure A.5, **II**). There was also no difference in the beginning years (2002–2004, $P = 0.706$), but there was a significant difference across the second period of observation (2014–2016; Table A.4, **II**).

The life stages of *G. imbricatus* were characterised by significantly different browsing proportions by different livestock in the first phase of restoration ($\chi2 = 145.76$, df = 2, $P < 0.001$). In total, 27% of juvenile individuals, 62% of vegetative individuals and 85% of generative individuals were browsed. Similar results were reported in the second phase (Table A.4, Figure A.5, **II**). In 2014, the proportion of browsed shoots in all plots grazed by cattle was higher than that in plots grazed by sheep, while in 2015 and 2016, the opposite was true.

There was a significant interaction between year, life stage and browsing proportion ($\chi2 = 10.86$, df = 2, $P < 0.005$). There were no differences in browsing between life stages in 2002, but in 2004, more individual plants in the vegetative and generative life stages were browsed than was anticipated by the null model ($P < 0.05$, FTD test). There was a significant interaction between management, life stage and browsing proportion ($\chi 2 = 8.03$, df = 2, $P < 0.02$). Fewer vegetative individuals in the sheep pasture were browsed, and a significantly higher number of vegetative and generative individuals in the cattle pasture were browsed ($P < 0.05$, FTD test) than was expected by the null model (**III**). In the second observation phase (2014–2016), the average browsing rate of juveniles was 45–50% for cattle and 15–40% for sheep. The average browsing rate for generative shoots was 70–100% in both treatments. The most significant difference was observed in 2016 for browsing of premature shoots, with an average of 5% for sheep and almost 100% for cattle (**II**).

5.3.3 Population performance

There was a gradual decline in population frequency within the sub-sites (across 1 x 1 m plots) under all grazing treatments (Figure 6, Table 1, right, **II**) as well as within abandoned plots in certain years. Specifically, the occurrence frequency dynamics of premature and generative plants differed between the mowing and sheep grazing treatments in the long term, although analogous trends were observed for juvenile plants (Figure 6C, **II**). Less evident but similar trends were also observed for cattle grazing plots. The same grazing trend was reported for premature plants, but the differences are not statistically significant (Figure 6B, **II**).

6. DISCUSSION

6.1 Coastal meadow recovery

6.1.1 Recovery time

Estonian legislation and management planning documents (Holm et al., 2019; Lotman and Rannap, 2020) state that coastal meadows can receive financial support for restoration from the national budget for one to three years, during which time restoration is expected. Then, these areas must enter the EU agri-environmental subsidy scheme, and management will be evaluated by the same criteria as any other semi-natural grassland. We claim that coastal meadows that have undergone restoration from abandonment can be considered as restored based on vegetation quality and in favourable conservation status only after ten years of constant management with suitable grazing pressure. The removal of secondary vegetation, such as reed and shrubs, in the first phase does not make a coastal meadow ecologically restored. Time and effort are needed to establish characteristic vegetation (Kose et al., 2020, **I**).

This problem is addressed by the new intervention measures designed by the Ministry of Rural Affairs and presented in the Estonian Common Agricultural Policy Strategic Plan. Additional finances can be applied in the first years after restoration for additional mowing activities if grazing has not been effective enough to suppress reed (Kask, 2020).

6.1.2 Coastal meadow recovery directions

The recovery time and arrival of habitat-specific species in coastal meadows are dependent on the meadow size, time of abandonment and edaphic conditions (Baur, 2014; Waldén et al., 2017; Winsa et al., 2015). All the restored areas that were adjacent to permanent meadows had the potential to move from managed to restored areas, and livestock that grazed both managed and permanent meadows had the potential to be seed vectors. In wetter areas (Piirumi, Kastna, Pürksi) (**I**) where the water table is high and there are many sediments and nutrients, reed has not fallen back. In Piirumi, communities dominated by sedge (*Carex disticha*) have replaced reedbeds instead of desired coastal meadow vegetation. The Piirumi and Pürksi sites had both been abandoned for a very long time (more than 30 and 60 years, respectively). Sammul et al. (2012) indicated that a longer period of time is needed for wetter sites to regain typical vegetation and suppress reed. Actions taken to restore grasslands have usually been intended to return to the past and achieve historical fidelity. Thus, prior studies examining such areas have used evaluation criteria such as structural replication, functional success and durability (Baker and Eckerberg, 2016). In our research, we examined post-abandonment restoration and tried to avoid a pre-abandonment focus for evaluation (Valkó et al., 2016) by comparing our results to permanent meadows, which served as reference areas that are undergoing the same environmental changes.

6.2 Restoration effects on vegetation parameters

Changes in vegetation at the treatment sites were compared to the reference sites in 2005 and 2015 in order to determine whether the restored meadows (restored either before or after 2005) achieved similar vegetation parameters to permanent meadows that were managed without major interruption for centuries (Tahu, Häädemeeste, Põgari, Haeska). The best quality indicators for coastal meadows are the coverage ratio of low-lying plants (more than 25%) and the proportion of these species (more than 23%) compared to the species pool. The ratios of medium-height plants (over 40%), light-demanding plants (more than 60%), salt tolerant plants, hemicryptophytes and cryptophytes (more than 60%) and wintergreen plants (more than 65%) in relation to overall plant coverage were also considered to be good indicators of the quality of coastal meadows (**I**), in line with Pätsch et al. (2019). These plants take time to appear during the restoration process (Waldén et al., 2017), regardless of whether degradation is characterised by tall herbs (Pakeman et al., 2017). Therefore, the main determinants of restoration success in this study were the replacement of *P. australis* and other water plants (EIV F10) by low-lying or medium-height, wintergreen, salt-tolerant and light-demanding species.

It is acknowledged that mowing contributes to species richness in many cases of semi-natural grassland management (Tälle et al., 2016). This notion was supported by our research; historically mown meadows had more species than historically grazed meadow parts. Often, the appearance of specific species or species richness are used as indicators of the restoration of semi-natural grasslands (e.g. Lindborg and Eriksson, 2004; Lundberg et al., 2017), although changes in the number of species cannot always be used as a restoration target (Bakker et al., 2000). Our research revealed that, in coastal meadows, species richness may not be the main indicator of quality. There is high diversity in the plant communities, associations and types that comprise coastal meadows due to variations in location around the Baltic Sea, bedrock, salinity, inundation and other factors (Pätsch et al., 2019). Some associations are more species-rich, and others are species-poor. We could debate the characteristics or derived diversity of species (Helm et al., 2015) and the availability of the species pool, but in our case, all restored meadows were near large permanently managed coastal meadows and connected to these meadows by cattle 'vectors'. Moreover, the species pool had few 'derived species', according to our observations at the research sites. Therefore, our research suggests that evenness is a better indicator of the quality of vegetation in coastal meadows than species richness, which is significantly higher in Estonian meadows compared to similar habitats on German and Danish coast (Wanner, 2009). As expected, permanent meadows showed high evenness, while during restoration activities, vegetation may include species from abandoned communities as well as recolonising meadow plants. Thus, the E index may be lower for meadows that are being restored.

In recent decades, the common reed has become a serious conservation problem because it has spread into ecologically valuable habitats and, as it is a strong competitor, it has eliminated most other species (Roosaluste, 2007, Wanner, 2009). Thus, suppression of reedbeds is crucial during coastal meadow restoration (Sammul et al., 2012). Our results confirm that by decreasing the amount of reed, the ratio of light-demanding, wintergreen, salt-tolerant and water-tolerant plants will increase significantly within 10 to 15 years. Currently, the height and presence of *P. australis* are used as indicators for quality estimations of coastal meadows under EU agri-environmental schemes that provide management subsidies. According to such schemes, reed stalks should be less than 50 cm tall (Lotman, 2011). However, the abundance of reed is not mentioned in management regulations. Our results showed that, in permanently managed meadows, reed comprised less than 2% of the vegetation coverage, while in meadows that have been restored from abandonment for 5, 10, or 16 years, reed comprised more than 2% of the vegetation coverage (**I**). The proportion decreases over time, but even meadows with a 16-year restoration history did not reach the threshold of 2% *P. australis* coverage. Therefore, our study revealed that the abundance (not only the height) of *P. australis* could be a good indicator of restoration success. Additionally, all measures to suppress reed while restoring coastal meadows from abandonment should be supported. This recommendation has been included in new Estonian national agricultural policy. Therefore, we suggest expanding simple field measurement methodology to include estimation of reed abundance in coastal meadows as well as vegetation parameters.

According to interviews with land managers, many methods have been used to suppress reed and shrubs during the early phase of restoration, such as burning reedbeds, mulching and cutting with grazing. Additionally, Roosaluste (2007) indicated that the competitive ability of common reed could be decreased through shading by other plant species, severe frosts in winter, serious drought during the vegetative period, strong wave and ice activity on the shore, grazing, mowing and burning. Mowing and burning techniques are described in detail by Huhta (2007) and we recommend to advise the land managers about these measures in more detail

6.3 Short- and long-term restoration effects on non-target species

Different restoration activities have effects on plants at the population level in both the short and long term. We studied these effects on a protected species, *G. imbricatus*, from 2002 to 2016. Evidently, the resumption of management shifted the population type from regressive to dynamic. Thus, as in other grassland species (e.g. Moora et al., 2003), the removal of plant biomass via grassland management enhanced the establishment of young *G. imbricatus* individuals. The strong positive response of the juvenile stage to management indicates that in the community under investigation, *G. imbricatus* is microsite- rather than diaspore-limited, and a proper management regime is needed for the restoration and conservation of viable local populations (**I**).

The increase in population density from 2002 to 2004 at the research sites was mainly due to the increased numbers of juvenile and vegetative individuals as well as the stable number of generative individuals. The mowing treatment resulted in a tenfold increase in the number of juveniles between 2002 and 2004 (the beginning of restoration), which was much more than the number reported in other years (see Figure 1 for 2014). The increase was probably inhduced by the increased availability of established microsites and improved light conditions for germination, as reported by Kostrakiewicz-Gierałt (2014a, 2014b).

The regeneration intensity in mown plots declined but stabilised after 10 years, and it remained at a higher level than before restoration began. This short-term positive reaction was confirmed in an observation from a nearby site in 2019, where long-term management of combined grazing and mowing led to the formation of tall sedge areas with only a few *G. imbricatus* specimens. The change in management to end-milling cutting in autumn 2018 led to an increase in juveniles (both bulbs and seedlings, as estimated from the excavated specimens) and flowering shoots in 2019. A similarly quick reaction of *G. imbricatus* to mowing was observed by Kubíkova and Zeidler (2011) in the Na Bystrem meadow in Moravia, and Canella et al (2020) reported similar results for *G. palustris* in the Alps.

Although the average density of *G. imbricatus* did not increase as a result of grazing treatments in the first three years of restoration, the population stage structure became more dynamic due to an increased share of juveniles. This response may be due to both enhanced seed dispersal and better establishment conditions in grazed and trampled vegetation. Although there is mixed evidence of whether grazing or mowing results in higher species richness in semi-natural grasslands (Kull and Zobel, 1991; Hansson and Fogelvors, 2000), population-level studies of grassland perennials have indicated that mowing after the flowering period, compared to grazing or mowing too early, may favour populations (Hegland et al., 2001; Brys et al., 2004). In 2020, an overall population study on 1000 ha in the Luitemaa Nature Reserve was carried out. More than one million specimens were estimated, which indicates good distribution over 20 years of restoration (Kose et al., 2021), with animal and human vectors from the very small and fragmented population remnants in the 2000s.

Usually, the mowing date is related to phenology, which, in Sweden, is based on the latitude and altitude of the site (Eriksson et al., 2015). In coastal areas of Estonia, phenology is greatly dependant on winter (ice) conditions on the coastal seas, which may occur over a week later than in the rest of the country (Ahas, 1999) and therefore haymaking is often not feasible before the beginning of July, according to personal communication with farmers (Kose et al., 2021). *G. imbricatus* usually flowers in the first week of July, and in coastal meadows, mowing is usually allowed from 15 July (because of breeding birds). This scheme favours *G. imbricatus* and its seed dispersal via mowing devices and aftermath grazing. Both haymaking machinery (Strykstra et al., 1997) and grazing animals (Fischer et al., 1996) are important seed vectors for species.

The dynamics of premature and flowering shoots were different from those of juveniles. In abandoned areas and both types of grazed areas, the number of specimens at both stages began to decline after the second year of the restoration. By 2004, the frequency of flowering shoots decreased from almost 100% to 20% in plots grazed by sheep. In abandoned areas, the number of flowering individuals declined in a similar way to the grazing treatments, but the plants were more evenly distributed in abandoned areas than in grazed areas.

The results of this research confirm the conclusions of earlier studies regarding the abandonment effect on *G. imbricatus* (Hänel and Müller, 2006; Kostrakiewicz-Gieralt, 2014b; Kubíkova and Zeidler, 2011; Richter, 2012). Plants become less abundant, but flowering shoots elongate in response to competition for light and pollinators. Consequently, *G. imbricatus* populations survive meadow abandonment and overgrowth for a rather long time. In contrast to the positive trends found by short-term counts, the re-survey of sites from 2012 to 2016 revealed that the population of *G. imbricatus* declined in grazed areas and continued to flourish only in mown plots. The contrast between the short- and long-term observations supports the objective assessment, which suggested that the goals of ecological restoration can be achieved only after 10 years of treatment (Joyce, 2014; Koch et al., 2017; Lundberg et al., 2017). These results warn against prematurely making conclusions regarding the degree of success in the early stages of restoration.

Different restoration measures applied to *G. imbricatus* led to differences in population performance after 15 years of management. Mowing is the only truly favourable management regime for *G. imbricatus*, as suggested by several other recent studies (Bonari et al., 2017; Tälle et al., 2018). It was recommended as normal management for the Häädemeeste region in the upper parts of coastal meadows by Kasvandik et al. (2003).

Previous research indicates that sheep browse *G. imbricatus* more selectively (61%) than cows (48%) (Kose and Moora, 2004). From 2014 to 2016, we observed that browsing habits differ annually, and while sheep browse almost half of juveniles from the grass, cows' browsing can vary yearly from 20–40%, despite similar availability of plants. Field observations indicated that after late grazing with sheep in 2003 and 2004, in the following years, a large number of *G. imbricatus* seedlings appeared near the paths of sheep and in their resting places. Similar zoochory (both endo- and epizoochory) was reported by land managers throughout the restoration period. The prescribed grazing pressure (0.8e1.2 LU/ha) was probably too high; Lyons et al. (2017) reported a long-term positive response to grazing pressure of 0.2 LU/ha in upland calcareous grasslands, although this is a habitat with much lower productivity. The low year-round horse grazing pressure (0.3 in the vegetation period and 0.2 in winter) was found to be favourable for rare species and communities in dry calcareous grasslands (Köhler et al., 2016), and it is recommended for dry sandy grasslands (Henning et al., 2017). On the other hand, Töth et al. (2018) suggest that livestock type is more crucial than grazing intensity in short-grass steppes and that sheep may be more selective grazers in cases of low grazing pressure (Töth et al., 2018). This could be the case for *G. imbricatus*.

6.4 Conservation and agricultural policies

6.4.1 Conservation

According to the final report "Evaluation of the Impact of the Common Agricultural Policy on Habitats, Landscapes, Biodiversity" (Alliance Environnement, 2019), all EU Habitats Directive habitats are either natural or semi-natural. Nearly all species listed in the Habitats Directive are dependent on semi-natural habitats, as are most species listed in the Bird Directive, although a number inhabit semi-improved/improved grasslands or low-intensity arable land.

From a conservation viewpoint, we suggest that management schemes favouring grassland biodiversity and rare plant species on coastal meadows must consider the grazing habits of available grazers, grazing pressure and timing. The diverse management patterns for grasslands have been suggested to be more effective for preserving arthropod diversity than monotonous management (Bucher et al., 2016), pollinators (Moron et al., 2008; van Klink et al., 2016), amphibians, breeding birds and feeding migratory waders (Arbeiter et al., 2018; Rannap et al., 2017). They are just as important for plants. Small- and large-scale heterogeneity is characteristic of natural ecological conditions, which must be considered while planning optimal restoration treatments (Valko et al., 2018; Wehn et al., 2018a, 2018b).

Our research revealed that the short-term part of our experiment produces an overly positive impression of the effectiveness of the restoration management support scheme. Long-term continuation of the same management types, however, shows their negative effect on restoration of the *G. imbricatus* population. Therefore, we suggest long-term monitoring schemes combined with restoration and recovery projects that focus on the whole range of ecosystem services and biodiversity issues rather than a single target species.

Since the beginning of the millennium, when restoration of semi-natural grasslands began, such activities have been financed from the Estonian national budget, EU-funded LIFE conservation projects or other structural funds, not the agri-environmental scheme (Kose et al., 2011; Holm et al., 2019). Also, Estonia has restricted restoration to Natura 2000 areas. Changes are not expected for the next programming period (2021–2027). However, Holm et al. (2019) strongly recommend changes such as increasing the scale of restoration (about 10 000 ha of coastal meadows are outside the Natura 2000 areas), improving the connectedness and manageability of existing and new restoration areas and increasing restoration of smaller areas landscapes that are difficult to access. Another problem is that the annual funds from the national budget allocated for coastal meadow restoration are too limited to fully cover the work, and therefore restoration outcomes may not be sufficient.

We recommend, in line with the Alliance Environnement (2019) report and Holm et al. (2019), enlarging the semi-natural grasslands restoration programme to areas outside Natura 2000 and improving the funding scheme to achieve better ecological results. We believe that a three-year period for restoration from long-term abandonment is not sufficient for an area to qualify as a permanent meadow (**III**). If national budgets are not able to support restoration activities for longer, the EU agri-environmental scheme should establish a three- to five-year transformation period for meadows still undergoing restoration to allow for additional reed suppression activities, like mowing, mulching and controlled burning.

The Drivers of Success study (Tucker et al., 2019) found that expanding conservation interventions to the wider environment is expensive, and Agri-Environment-Climate Measure budgets are often insufficient to cover areas beyond the Natura 2000 network or other targeted areas. As a result, more funding and targeting of schemes to species and habitats is required to increase the scale and effectiveness of agri-environmental scheme and thus achieve landscape- and population-level improvements.

Until now, additional mowing could be applied without extra payment upon the approval of a conservationist if the area is 50% grazed to short vegetation and there is a need for additional biomass removal for any reason. Upon entering the agri-environmental scheme, freshly restored coastal meadows should be subject to additional intervention measures to fight reed and shrubs, without strict preconditions, if the areas are wet and were abandoned for long time (more than 10 years).

6.4.2 Policy

Semi-natural grasslands and similar habitats are by far the most important agricultural habitats for biodiversity, both in general (e.g. species richness) and for Birds and Habitats Directive habitats and species in particular. Therefore, to make the most effective progress toward general biodiversity goals, it is necessary to ensure that the key factors affecting biodiversity in these habitats are addressed by Common Agricultural Policy instruments and measures, and that they are implemented for a high proportion of the habitats (Alliance Environnement, 2019).

Our research, in line with that of Alliance Environnement (2019) and Holm et al. (2019), suggests that area-based support schemes are not sufficient to protect biodiversity as a whole. The benefits to biodiversity are strongly context-dependent, and the positive outcome for overall biodiversity can be questionable. Therefore, the new Estonian semi-natural grasslands intervention measures, which combine hybrid measures with quality-based incentives, are very welcome. Hopefully, they will include strong criteria for assessing different aspects of biodiversity as quality criteria for permanently managed meadows and those that have been restored and are gradually improving. We suggest considering one-time zoning efforts for finding relevant species and criteria for coastal meadows based on their vegetation types (e.g. Pätsch et al., 2019) We also recommend including functional traits in the assessment scheme.

It is important to clarify the terms of restoration and recovery in Estonian intervention measures (Kask, 2020), as they are present in agri-environmental scheme but not clarified. We suggest that a coastal meadow may be 'restored' in terms of the activities carried out, its vegetation and biodiversity may not recover for 10 to 20 years. We also recommend basing the criteria for coastal meadows' quality on targets rather than means, in accordance with Bakker et al. (2000) as today the evaluation of coastal meadow management is based on hectares, animal units and grazing time.

Cancelling of restoration activities or the choice to not enter the agri-environmental scheme for meadows that have undergone restoration may be a result of poor consultancy and a lack of an advisory system (Holm, et al., 2019). We suggest that, for coastal meadows, such problems may also result from poor recognition of vegetation and plant communities.

7. CONCLUSIONS

The restoration of semi-natural grasslands in Estonia is a new nature conservation activity with only 20 years of history. Coastal meadows were among the first habitats to undergo restoration with the aid of international projects in the late 1990s. While the restoration activities and methods used for coastal meadows in Estonia have been elaborated upon and tested many times, the methodology for evaluating success and the biodiversity assessment criteria are not sufficient. One reason may be that coastal meadow habitats and plant communities vary in different parts of Estonia and are very complex, making it difficult to identify good indicators for vegetation assessment.

We argue that the existing area-based evaluation methodology and the monitoring of the colonisation and breeding rate of target species (birds and amphibians) in coastal meadows are insufficient to evaluate the recovery of coastal meadows as habitats. They do not consider the real situation of vegetation, including its quality or suitability for supporting the target species. The indicators used for assessment of coastal meadow vegetation are quantitative (area, height of vegetation, amount of litter) and do not consider quality issues regarding plant cover.

This thesis is a synthesis of 20 years of research into the restoration and recovery of Estonian coastal meadows. Our observations and conclusions are as follows:

1) Recovery of coastal meadow vegetation from reed and bush encroachment resulting from land abandonment may take decades. In the best cases, vegetation may recover and become similar to well-maintained meadows in 15 years. This is not enough for meadows that are wetter and have been abandoned for longer periods.
   The plant communities of coastal meadows close to the shoreline that have mainly been grazed are not as species-rich as the plant communities that are at higher elevations and are more distant from shore, which have historically been used for haymaking and aftermath grazing.
   Edaphic changes have led to paludification and massive reedbeds, and restoration may result in, for example, sedge communities instead of desired coastal meadow plant communities.

Our study suggests some measurable vegetation quality targets, which are totally missing in current conservation practice, for evaluation of coastal meadow restoration. We claim that coastal meadows that have undergone restoration from abandonment can be considered as restored (based on vegetation quality) and in favourable conservation status only after at least 10 years of constant management with suitable grazing pressure. The removal of secondary vegetation, such as reed and shrubs, in the first phase of restoration does not make a coastal meadow restored. Time and effort are needed to establish characteristic vegetation.

2) It is essential to develop a long-term monitoring plan that begins with restoration activities and follows the recovery process, as the effects of short- and long-term restoration as well as different restoration activities may vary or be misleading.
   When a seed bank is present, restoration activities and disturbances may give a short time advantage to species that reproduce with seeds, bulbs and rhizomes, like *G. imbricatus.*
   Mowing is the best measure for supporting the populations of tall perennial herbs, while grazing is the most recognised measure for restoration and maintenance of ecological grassland. When implementing grazing as a conservation tool, the suitable grazing pressure should be adjusted to sustain protected plant species. Such adjustments could include mosaic grazing patterns or the one-fifth grazing rotation scheme, in which one-fifth of area is not grazed each year.

3) To restore and maintain coastal meadows in Estonia, policies should target the whole range of ecosystem services and biodiversity issues, rather than focusing on single species.
   We believe that a three-year period for restoration from long-term abandonment is not sufficient for an area to become restored in ecological terms. When joining the agri-environmental scheme, additional reed suppression activities, like mowing, mulching and controlled burning, should be available for the first few years, with minor bureaucracy for farmers.
   The payments for coastal meadow restoration and management applied in the previous program period did not take into account the time, effort and resources required for these activities, and therefore, the desired results were not achieved. We hope that all additional

measures planned in new interventions for semi-natural grasslands will be implemented from 2021 onward, and that the payment rates will be carefully considered in order to meet real expenses and demands.
Semi-natural grasslands, especially coastal meadows, lack a quality estimation system, as no good, simple and easily applicable criteria have been developed. We believe the new agri-environmental scheme intervention measure for semi-natural grasslands, which elaborates and tests the hybrid scheme, is very necessary. We suggest that one quality criteria could be less than 2% coverage of common reed.

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SUMMARY IN ESTONIAN

Läänemere-äärsed rannaniidud on poollooduslikud kooslused, millel on suur looduskaitseline väärtus nii Eestis kui ka Euroopa Liidus (EL). Poollooduslikke kooslusi nimetatakse ka pärandkooslusteks, sest need on enamasti püsirohumaad, mille looduslik suktsessioon on peatatud pikaajalise ekstensiivse põllumajandustegevuse, st niitmise ja karjatamisega. 1900. aastate alguses oli sel viisil kasutatavaid rannaniite kuni 35 000 hektarit. Kuna rannikul asuvad rohumaad on seotud keeruliste loodusolude ja sageli tükeldatud maaomandiga, ei ole need tavapärases põllumajanduses muljetavaldavad ning on 1940. aastatest saadik järk-järgult kasutusest välja jäänud. 2000. aastate alguses kasutati veel vaid 5100 hektarit. Poollooduslike koosluste, sealhulgas rannaniitude taastamine ja hooldamine on viimasel kahel kümnendil olnud Eesti looduskaitse auasi, kuid samad probleemid seisavad ka teiste Läänemere-äärsete riikide ees, kus maakasutusmuutused, peamiselt kasutusest väljalangemine, on põhjustanud nende koosluste kadu ja olukorra halvenemist suurtel aladel.

Rannaniitude taastamistegevusel on kindlad eesmärgid: suurendada rannaniitude pindala, ühendada üksteisest eemalolevaid ja säilinud fragmente ning toetada sihtliikide, nagu kõre, roheka õõskeele, rannaniidul kurvitsaliste ja läbirändavate lindude populatsioonide heaolu või asustamise laienemist. Rannaniidu taimekooslustele ja nende taastumisele on vähe tähelepanu pööratud. Enamasti rahastavad rannaniitude taastamist Eesti riik ja/või ühekordsed projektid ning eesmärk on taastamistegevuste kiire elluviimine, et olla EL-i ühtse põllumajanduspoliitika põllumajandus- ja keskkonnatoetuste jaoks toetuskõlblik. Seetõttu on kriteeriumid lihtsad. Mõõdetakse peamiselt taimkatte (sh pilliroo) kõrgust ja madalmuruse taimkatte osakaalu, mis on ainsad taimkatte seisundi näitajad. Samal ajal seiravad looduskaitseorganisatsioonid väga detailselt sihtliike, et hinnata nende asurkondade seisundit ja taastumist. Poollooduslike koosluste taastamine on Eesti looduskaitses suhteliselt uudne tegevus, mille kogemust on riigis vaid 20 aasta jagu. Rannaniidud olid ühed esimesed kooslused, mille taastamisega alustati rahvusvaheliste projektide ja kogemuste toel 1990. aastate lõpus. Kui taastamismeetmeid on kogu protsessi vältel juurutatud ja täiendatud, siis taastamise edukuse ja taastumise hindamise meetodid on ebapiisavad ega kata rannaniitude kogu elurikkust. Üks põhjusi võib olla see, et Eesti rannaniitude taimekooslused on Eesti erinevates piirkondades väga varieeruvad ning see muudab ühtsete ja heade indikaatorite leidmise raskeks.

Võib väita, et kasutusel olev pindalapõhine hindamismetoodika ei ole piisav ning vaid sihtliikide (kahepaiksed ja linnud) taasasustamise ja paljunemise edukuse seiramine ei anna ülevaadet sellest, kas taimekooslused kui elupaigad on vajalikul määral taastunud, et olla kvaliteetsed ja sobilikud elupaigad järgmistele troofilistele tasemetele. Kvantitatiivsed indikaatorid, nagu pindala, taimkatte kõrgus ja kulu hulk, ei võta arvesse taimkatte liigilist koosseisu ega sellistele niitudele iseloomulikku kamardumist.

Liigirikkus ja liigiline koosseis on taastamistööde edukuse hindamisel tavapärased hindamiskriteeriumid. Rannaniitude taastumise kvaliteeti on aga sellisel viisil keeruline hinnata, sest rannaniitudel esineb palju erinevaid kooslusi, mis on väga varieeruvad ja mosaiiksed. Väga raske on leida häid indikaatorliike, mis oleksid igal rannaniidul igas koosluses olemas ja kirjeldaksid samal ajal rannaniidu taimkatte head seisundit.

Käesoleva töö ajendiks said 2013. aastal Eestis rakendatavad rannaniitude taastamise ja hooldamise põhimõtted ning normid, milles ei arvestatud kõiki rannaniitude väärtusi ja taastamise ning taastumise asjaolusid. Seetõttu tekkisid käärid reaalse olukorra ja määruste vahel. Kuigi rannaniitusid on taastatud ligi kaks kümnendit, näitavad sihtliikide seire tulemused nende kesist seisundit ja asurkondade aeglast taastumist. Töös keskendutakse rannaniitude taimekoosluste taastamisele ja taastumisele, sellele, kui kaua võiks taastumine aega võtta ning milliste kriteeriumite alusel saaks hinnata taimekoosluse taastumist või seisundit rannaniidul. Hindame pikaajaliste eksperimentide varal erinevate taastamistegevuste lühi- ja pikaajalist mõju rannaniidul elutsevale kaitsealusele taimeliigile niidu-kuremõõgale, kuid ei ole samas taastamistegevuste planeerimisel sihtliik.

Töö sihtpunkt oli uurida rannaniidu taimkatte taastumise kiirust ja võimalikke kriteeriume taastumise hindamiseks (**I**) ning selgitada mittesihtliigi vastust erinevatele taastamistegevustele lühikese ja pika aja jooksul, et mõista, kas kõik rannaniidu taastamis- ja hooldusvõtted sobivad haruldastele taimeliikidele (**II** ja **III**). Peale selle otsiti erinevaid võimalusi olemasolevate looduskaitseliste ja põllumajanduslike keskkonnameetmete parendamiseks rannaniitude taastamise ning hooldamise paindlikumaks ja tulemuslikumaks muutmisel, et toetada kogu elurikkust ja ökosüsteemi teenuseid. (**I**, **II** ja **III**)

Töö eesmärgid:

1. Tuvastada rannaniitude taastumiseks kuluv aeg: kui kaua kulub rannaniidu taimkattel taastumiseks ja kuidas seda hinnata? (**III**)
   H 1. Rannaniidu taimkatte struktuuri taastumine sõltub ajast, kui kaua ei ole ala kasutatud.
   H 2. Pikka aega ja pidevalt majandatud rannaniidud on rannaniitude taastumise hindamisel hea võrdlusmaterjal.

2. Uurida erinevate lühi- ja pikaajaliste taastamistegevuste mõju populatsiooni tasemel niidu-kuremõõga näitel, mis on looduskaitsealune liik, kuid ei ole rannaniidu taastamisel sihtliik. (**II** ja **III**)
   H 3. Kõik taastamismeetmed (niitmine, lammaste ja veiste karjatamine) avaldavad taastamistegevuste alguses kiiret positiivset mõju niidu-kuremõõga populatsiooni suurenemisele.
   H 4. Pikaajalise taastamise ja majandamise käigus on erinevate majandamisviiside mõju niidu-kuremõõga populatsiooni seisundile ning püsimisele erinev.

3. Anda oma töödele ja erinevate autorite publikatsioonidele toetudes ülevaade, kuidas toetusmeetmed ning seadused ja EL-i ühtse põllumajanduspoliitika meetmed saaksid paremini toetada rannaniitude elurikkuse eesmärkide täitmist. (**I**, **II** ja **III**)

Töö eesmärkide saavutamiseks tehti kordusuuringuid kahe 2002–2005. aastal läbi viidud uuringu raames, et tuvastada taastamise järel ligi kümne aasta vältel toimunud muutused.

Töö tulemused aitavad paremini mõista poollooduslike koosluste taastamisele ja taastumisele kuluvat aega ning võimaldavad paremini seada taastamistööde eesmärke ja hindamiskriteeriume.

Ligi 20-aastase rannaniitude praktilise taastamise ja uurimistöö ning kirjanduse toel jõuti järgmiste tulemusteni.

Rannaniitude taimkatte taastumine koosluse hülgamise tagajärjel laienevalt kasvavast pilliroost ja võsast võib võtta aega aastakümneid. Parimal juhul võib taimkate uuritud aladel taastuda ja muutuda sarnaseks pikka aega kasutuses olevate niitudega 15 aasta jooksul vaid kahel juhul kolmest. See aeg ei ole kindlasti piisav niiskemate ja pikka aega kasutamata rannaniitudele. Veepiirile lähemal asuvad ja peamiselt karjatatavad taimekooslused ei ole nii liigirikkad kui need, mis on veepiirist kaugemal ja mida on ajalooliselt kasutatud heina varumiseks. Muutunud keskkonnatingimused on sageli viinud rannaniitude soostumiseni ja massiivsete roostike pealetungini. Sellisest olukorrast taastumine võib soovitud rannaniidutaimestiku arendamise asemel viia hoopis tarna- või muude koosluste tekkeni.

Taimkatte taastumise hindamiseks soovitame lisaks pindalapõhistele kriteeriumitele kasutada ka kvaliteeti kirjeldavaid tunnuseid, mis looduskaitsepraktikas praegu puuduvad. Hülgamisjärgse kuni kolmeaastase taastamisprotsessi läbinud niidud jõuavad taimkatte taastumiseni. Soodsasse looduskaitselisse seisundisse jõutakse pärast vähemalt kümneaastast pidevat sobiva karjatamiskoormusega majandamist. Esmane taastamine ehk pilliroo ja võsa eemaldamine ei taasta veel rannaniitu ning iseloomuliku taimkatte kujunemine nõuab aega ja pingutusi.

Selleks, et taastamistegevusi ja taastumist hinnata, on vajalik pikaajaline seireplaan, mis lükatakse käima koos taastamistegevustega, sest lühi- ja pikaajalistel ning erinevat liiki taastamistegevustel võib olla erinev mõju ja lühiajalise ning selektiivse seire tulemused võivad kogu elurikkuse hindamisel olla eksitavad. Kui seemnepank on olemas, siis võivad taastamistegevused ja häiringud anda edumaa liikidele, kes paljunevad seemnete, sibulate ja risoomidega, nagu niidu-kuremõõk. Niitmist peetakse kõrgekasvulistele püsikutele sobivaimaks majandamisviisiks, kuigi rohumaade ja rannaniitude ökoloogilise taastamise ning hooldamise jaoks on soovitatav karjatamine. Seega, kui karjatamist soovitakse kasutada looduskaitsemeetmena, on vajalik reguleerida karjatamiskoormusi või rakendada sobivaid karjatamismustreid, et toetada kõigi kaitsealuste taimeliikide püsimist.

Rannaniitude taastamise eesmärkide seadmisel on vajalik arvestada ka taimkatte taastamise ja taastumise protsesse ning ainult sihtliikidele keskendumise asemel peab arvestama ja toetama kogu elurikkust ning ökosüsteemiteenuseid. Veel soovitame, et kõikidel niitudel, mis sobituvad taastamisest püsirohumaana EL-i ühtse põllumajanduspoliitika toetuste skeemi, peaks esimestel aastatel olema võimalus pilliroogu ja võsa nende tõrjumiseks niita. Seda on käesoleva perioodi sekkumislehes arvestatud. Loodetavasti niitmise lisameede jõustub ja on maahooldajatele kergesti kättesaadav. Kuna alanud perioodi sekkumisleht ja meetmed on alles väljatöötamisjärgus ning kvaliteedipõhise lisatoetuse meetmete juurutamine on kavas, siis soovitame pärast soovitud sihtliikide leidmist lisada kvaliteedinäitajaks ka pilliroo katvuse hindamise ja taimkatet kirjeldavad parameetrid.

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I

ORIGINAL PUBLICATIONS

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RESEARCH ARTICLE

Twenty years of Baltic Boreal coastal meadow restoration: has it been long enough?

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The restoration of a threatened type of seminatural grassland—the Baltic Boreal coastal meadows—began in Estonia in 1997. The main causes of degradation of these communities were land abandonment and overgrowth by reed. In 2015, we resurveyed 14 sites and classified as (1) permanently managed or (2) restored before 2005, or (3) after 2005. In 2015, all sites were managed under the EU agri-environmental scheme and classified as permanently managed or restored before or after 2005. The resurvey focused on assessment of the long-term success of restoration, comparing the vegetation parameters of restored meadows with permanently managed meadows (which were considered as reference). Our study revealed that historical management patterns have an impact on the species richness of these habitats, as more species were found in historically mown meadows, even if the sites were restored by grazing. However, species richness was not an important indicator of coastal meadow recovery. The best indicators of restoration success are evenness and coverage of low-lying, light-demanding, salt-tolerant, wintergreen, cryptophyte, and hemicryptophyte plant species. *Phragmites australis* is a good indicator species for the habitat, as its abundance indicates poor habitat quality. The study indicated that the recovery of coastal meadow habitat from abandonment requires more than 15 years of restoration activities, and suggested the 3-year restoration period covered by conservation measures and funds is not enough. Therefore, we recommend that agri-environmental schemes should support additional restoration activities for recently restored meadows which are entering the management scheme.

Key words: functional traits, land abandonment, recovery time, restoration success, resurvey, seminatural grassland

Implications for Practice

- The restoration of coastal meadow vegetation after abandonment requires more than 15 years to achieve vegetation parameters and quality similar to permanently managed meadows. Active restoration measures, like additional mowing, mulching, and controlled burning, should be applied in management schemes for the whole restoration period in addition to grazing, which is usually the main restoration measure.
- Coastal meadows are very diverse, and therefore the success of their restoration is difficult to measure based on the occurrence of specific plant species. *Phragmites australis* coverage indicates poor habitat quality and vegetation functional characteristics are good indicators of the success and quality of coastal meadow restoration.

Introduction

Coastal grasslands around the Baltic Sea (referred to as the Baltic Boreal coastal meadows, or simply as coastal meadows) are among the most threatened habitats in Europe (Joyce 2014; Rannap et al. 2017). They are listed as a priority habitat in Annex I of the EU Habitats Directive (92/43/EEC) due to their rapid decline in the second half of the twentieth century (Lotman & Lepik 2004). Their high conservation value, the ecosystem services they provide, and their species richness have motivated restoration and management activities in the last few decades (Wanner 2009; Sammul et al. 2012).

In Estonia, the area of coastal meadows under management was reduced from 29,000 ha in the 1960s to 9,500 ha in 1981. By 2000, the area of managed coastal meadows had decreased to 5,100 ha (Luhamaa et al. 2001). The degradation of these habitats is caused by land abandonment followed by reed (*Phragmites australis*) encroachment, which is typical in the Baltic Sea region. The first attempts to restore the coastal meadows took place in 1997 in Matsalu National Park (Lotman et al. 2014). Since then, restoration and management activities have increased slowly but steadily. By the end of 2019, 10,700 ha of coastal meadows were managed under the EU agri-environmental scheme. This area consists of about 5,100 ha of area that has been managed permanently for centuries and

Author contributions: MK, KT conceived and designed the research; MK, KK performed the fieldwork; KH, KT, MK analyzed the data; all authors wrote and edited the manuscript.

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5,600 ha that has been reclaimed from abandonment through restoration activities since 2000. An additional 1,100 ha of coastal meadows were under restoration in Estonia at the end of 2019 as part of activities initiated less than 3 years before 2019 and supported by designated national funding. The main restoration measures that are applicable to coastal meadows in Estonia are described in detail by Lotman and Lepik (2004) and revised in the Estonian coastal meadows' management plan (Lotman 2011). The coastal meadow in favorable conservation status has no trees and shrubs; it has low vegetation, created by grazing or mowing. Some management patterns with different animals and mowing strategies are described by Kose et al. (2019). A common restoration practice is to actively destroy reed and clean the meadows from shrubs by mowing or mulching to enable the reintroduction of grazing as soon as possible and improve light conditions for coastal grassland-specific plant species to encourage their establishment and spreading. Typically, it takes 2 to 3 years to clean the meadows of shrubs and dead reed and to sufficiently suppress reed growth to enable grazing and allow the area to enter the EU agri-environmental scheme for seminatural habitat management. In total, 5,600 ha of coastal meadows that had undergone this short process of restoration qualify as "managed meadows" rather than "restored" or "under restoration." The evaluation criteria for entering the EU agri-environmental scheme are the proportion of short vegetation (more than 50% of the area) and the height of reed in the late summer (less than 50 cm). Usually, corrective mowing or mulching in the late summer is needed in the first 5 years to suppress reed and meet the criteria (Lotman 2011).

Sammul et al. (2012) indicated that after 5 years of coastal meadow restoration, some desired or typical species had returned to the research areas, but the height of vegetation and cover of common reed were not suppressed, and delays in restoration success in wetter and more nutrient-rich areas could be observed, indicating site-specificity. During a 5-year experiment, Berg et al. (2011) reported an increase in bare ground during the first few years of coastal meadow restoration due to mowing and only small changes in vegetation parameters. Some positive impacts on species diversity in grasslands were reported after 5–10 years of management. For example, positive impacts were reported by Bakker et al. (2003) for natural and artificial salt marshes in the Wadden Sea area, Lindborg and Eriksson (2004) for Swedish seminatural grasslands, Kose et al. (2019) for Estonian coastal meadows, and Lundberg et al. (2017) for coastal dune meadows in Norway. These results suggest that trends in diversity can be detected after a longer restoration period. Other authors also mention that long periods of time are needed for restoration, but they do not indicate whether these periods are years, decades, or centuries in length (Török & Helm 2017). However, they do suggest that the longer the period of abandonment is, the longer, more challenging, expensive, and time-consuming the restoration process will be (Valkó et al. 2018).

To date, the main targets of coastal meadow restoration have been endangered bird and amphibian species (Hellström & Berg 2001; Rannap et al. 2007; Durant et al. 2008; Zmihorski et al. 2016). However, many papers note that neither restoration nor conservational management has achieved the desired results in terms of the restored area, quality, or recolonization of coastal meadow specialist bird and amphibian species (Raatikainen et al. 2017; Rannap et al. 2017). Other studies have indicated the need for more measurable goals related to vegetation recovery (Bakker et al. 2000; Gustavsson et al. 2011; Walden & Lindborg 2016; Török & Helm 2017). As it is presumed that endangered bird and amphibian species recolonize meadows after vegetation functionality has recovered, it is reasonable to evaluate the speed and course of restoration based on the characteristics of plant communities (Baur 2014).

Plant species composition and richness have been used as the main indicators in evaluations of grassland management and restoration (Baur 2014; Horrocks et al. 2016; Walden & Lindborg 2016). It is well known that grazing increases species richness as grazing reduces competition for light and small growth species have growth opportunities while in the absence of management, these communities experience a decline in the species richness of vascular plants (e.g. Rosen 1982; Kull & Zobel 1991) as abandonment gives way to successional changes and in coastal grasslands it means overgrowing by reed in first phase. Typically, richness (S), or number of species, is considered the simplest metric used to represent diversity, and it is the most commonly applied. Normally, coastal meadows do not show very high measures of plant species diversity on a small scale, as their species pool in communities is 28–53 (Pärtel et al. 2007). Lower values than that usually reflect a high proportion of reed (or other tall grasses) in a meadow. A coastal meadow with good conservation status should exhibit high evenness (E) in terms of the distribution of species across the area (e.g. Berg et al. 2011).

Some authors have shown that concentrating on fixed species makes it more difficult to compare sites and regions and have suggested that studying functional characteristics could be a solution (Kahmen & Poschlod 2008; Török & Helm 2017). Some functional characteristics respond to management (Bullock et al. 2001; Kahmen & Poschlod 2008; Wellstein et al. 2011; Koch et al. 2017), such as plant height, which is usually considered a surrogate for competitive ability (Violle et al. 2007). Adult plant height is the most common measure of whole-plant size, and it indicates the ability to preempt resources and outcompete other species (Díaz et al. 2015). It also reflects grazing tolerance, a short lifespan, and stoloniferous and rosette growth (Diaz et al. 2004). The plant identification literature can be a good source for retaining information on plant height. In Estonia, the main literature is the Estonian Plant Identification Book (Krall et al. 2010), which contains the average and maximum heights of species. These figures can be referred to as plants' theoretical height. The coverage ratio of high- and low-growing plants should reflect how long and how effectively the area has been managed, as a species-rich coastal meadow mostly consists of low-growing plant species. Although historically the meadows were used as pastures for all domestic animals—and, in some cases, for haymaking—nowadays, beef cattle are preferred for restoration and habitat management purposes (Sammul et al. 2012; Laurila et al. 2015). No differences in management results for biodiversity have been detected (Laurila et al. 2015).

To better understand and describe the abiotic conditions at the sampling locations, the Ellenberg species indicator values (EIVs; Ellenberg et al. 1991) are often used for grasslands (Kladivová & Münzbergová 2016; Hülber et al. 2017; Benthien et al. 2018). The EIVs describe the site conditions of these meadows, using plants as indicators for soil parameters such as pH, nitrogen (fertility), humidity, salinity, climatic continentality, light availability, and temperature. The selected values—salt tolerance (S), humidity tolerance (F), and light demand (L)—are specific to coastal meadows.

Due to the huge efforts put into coastal meadow restoration in Estonia (Kose et al. 2011) and doubts about the EU Common Agricultural Policy's (CAP's) ability to support achievement biodiversity targets (Pe'er et al. 2014), there is a need to understand the key factors that affect the success of restoration of coastal meadow vegetation. In addition, it is necessary to find simple and measurable indicators for the evaluation of restoration success and to understand the thresholds of an effectively recovered community.

Our study makes use of 10-year-old data (Sammul et al. 2012) and repeats a survey of the same locations that were examined in a previous study. We aim to answer the following questions: (1) On what time scale can coastal meadow vegetation be restored? (2) What are the measurable indicators and vegetation characteristics of restored/well-maintained coastal meadow communities?

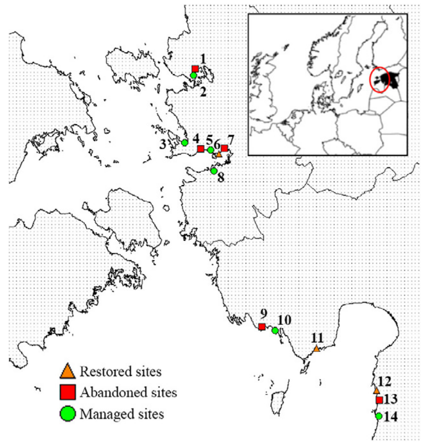

Figure 1. Map of the study areas with different management regimes. The characteristics of the sites are in Table S1 (management regimes from 2005 defined by Sammul et al. 2012). Silma region (1–2), Matsalu region (2–8), Tõstamaa region (9–11), and Häädemeeste region (12–14).

Methods

Study Area

The study was carried out by resampling 14 meadow sites on the western coast of Estonia examined by Sammul et al. (2012). In 2005, these meadow sites were selected in four coastal regions along the coastline of mainland Estonia (Fig. 1).

Each region had at least one permanently managed meadow, one abandoned meadow, and one meadow undergoing a restoration process, except Silma, in which there were only managed and abandoned meadows. Within each region, the meadows were selected to be as close as possible to each other, and sampling was done in carefully selected parts of the meadows in order to avoid elevation gradients and salinity differences. Plant communities were identified as the *Molinia caerulea-Carex panicea* type of the *Armerion maritimae* association in the Silma region and the *C. panicea-Galium palustre* and *Filipendula ulmaria* types of the *Triglochino-Agrostietum stoloniferae* and *Molinio-Arrhenatheretea* associations (Pätsch et al. 2019). These communities are distinct and rare vegetation types and are restricted to the northern Baltic Sea (the West Estonian archipelago) and Baltic Proper (Pätsch et al. 2019).

In this article, the analyzed meadows were divided into three management groups depending on their management and restoration time (Table S1, Supporting Information). Information about the management history was obtained from interviews with land managers and conservation officers. Meadows that had been permanently managed for centuries, or at least since 1940 (before World War II), were classified as "permanent meadows" and were used as references in analyses (see pictures of meadows in different restoration stages in Fig. S8). The second group included meadows for which restoration had started before 2005, when Sammul et al. performed sampling. These are referred to as "meadows restored before 2005." The meadows for which restoration started after 2005 (i.e. were abandoned in 2005) are referred to as "meadows restored after 2005." Table S1 describes the main features of each meadow and its management history. In 2015, all meadows were managed as permanent meadows under the EU agri-environmental scheme. Meadows identified as "favorable" in Table S1 feature low sward resulting from management activities, the presence of coastal meadow species, and the absence of reed stands in the lower parts of the meadow (Lotman 2011). Reed may also be present in favorable condition meadows, but it cannot form solid stands. Meadows qualifying as "extremely poor" have dominant monotonous reed stands (usually higher than 1.5 m), no continuous grass layer, and typical coastal meadow plants. All other situations, such as those in which reed was present to a large extent but suppressed by restoration activities, coastal meadow plants formed the permanent grass layer, and vegetation height was 40–100 cm, were considered "poor" (Table S1). Estimations were made by the authors during fieldwork and through consultation with conservation officers.

Field Sampling and Data Collection

In general, the same study protocol was used in both 2005 and 2015 (see Sammul et al. 2012). All plots were marked with GPS coordinates in 2005, and the same coordinates were used in 2015, acknowledging the range of GPS measurement accuracy. In both cases, two 100-m transects located 30 m apart were sampled from each site. In July 2015, ten 0.5 × 0.5–m plots were thoroughly analyzed in each transect to identify all vascular plant species in the plot, their coverage, total coverage, and the maximum and medium heights of vegetation.

Analyzed Factors

In the general linear model (GLM) and principal component analyses (PCA), several additional factors were calculated for the plots: the total number of species in a meadow, average EIVs for light availability (L), salinity (S), humidity (F), and water plants (F10), and the percentages of different life forms in the plots, such as hemicryptophytes (H) and chamaephytes (C) (Raunkiær 1934) as well as wintergreen plants. Two factors in the analysis were used to indicate salt tolerance: moderately salt-tolerant plants (EIV 4–5) and salt-tolerant plants (EIV 7–9). No species with an EIV of 6 were present in the meadows. We used the theoretical vegetation height (from Krall et al. 2010) to identify low-lying plants (theoretical average height up to 25 cm) and medium-height plants (theoretical average height of 26–50 cm). We used Shannon indices since they were used by Sammul et al. (2012), whose data and experiment set we reused. The coverage of *Phragmites australis* was included as a factor in the analysis.

Data Analysis

The statistical analyses were carried out with SAS 9.4 software (SAS Institute Inc., Cary, NC, U.S.A.). Correlations between the variables were analyzed with the SAS GLM. We analyzed the impact of the management group (permanently managed, restored before or after 2005) in 2005 and 2015 on different plant community characteristics: average plant coverage (%), summarized plant coverage of all species in the plot, number of species per plot, average height of vegetation, maximum height of vegetation, ratio of low-lying plants, ratio of medium-height plants, Shannon H, Shannon E, ratio of moderately salt-tolerant plants, ratio of salt-tolerant plants, ratio of humidity-tolerant plants, ratio of water plants, ratio of light-demanding plants, ratio of hemicryptophytes and cryptophytes, ratio of wintergreen plants, ratio of *P. australis*, and species pool. Analysis was performed with an analysis of variance (ANOVA) multiple-analysis tool (n = 259) as well as a Ryan-Einot-Gabriel-Welsch (REGW) posthoc test. We considered the data from each plot to be independent observations and status to be a fixed factor with three levels. The dynamics of community characteristics were studied with a covariation analysis (community characteristic*year), and the statistically significant

Table 1. The average values of the studied factors, which are grouped by management status, in 2005 (n = 120, 60, and 100 plots per group for groups: permanently managed, restored before and after 2005, respectively). Significant differences were revealed by REGWQ tests in particular year by management regimes. Statistically significant differences were marked with various shades of gray, while the darkest indicated the highest value. All ratios in current table are calculated plotwise based on coverage. a ab b c.

Year	*2005*			*2015*		
Management Group	*Permanently Managed*	*Restored Before 2005*	*Abandoned (Restored After 2005)*	*Permanently Managed*	*Restored Before 2005*	*Restored After 2005*
Number of species per plot (average)	10.2	9.2	7.8	9.8	9.3	8.8
Shannon H	1.78	1.56	1.35	1.75	1.61	1.56
Shannon E	0.8	0.72	0.67	0.79	0.74	0.76
Average plant coverage (%)	63	57	72	68	61	56
Average height of vegetation (cm)	16	19	106	22	32	45
Maximum height of vegetation (cm)	36	52	161	48	67	87
Coverage of low-lying plants (theoretical height up to 25 cm) from overall species pool (%)	25.12	16.49	0.8	23.03	19.75	17.37
Ratio of low-lying plants (theoretical height up to 25 cm)	0.5	0.1	0.08	0.27	0.11	0.1
Ratio of medium-height plants (theoretical height 26–50 cm)	0.42	0.58	0.24	0.55	0.51	0.39
Phragmites australis coverage (%)	<1	7	30	<1	10	20
Ratio of light-demanding plants	0.68	0.65	0.35	0.6	0.58	0.54
Ratio of humidity-tolerant plants	0.46	0.72	0.38	0.57	0.62	0.46
Ratio of moderately salt-tolerant plants	0.02	0.06	0.02	0.07	0.05	0.01
Ratio of salt-tolerant plants	0.46	0.01	0.09	0.22	0.13	0.08
Ratio of hemicryptophytes and cryptophytes	0.64	0.62	0.41	0.64	0.61	0.46
Ratio of wintergreen plants	0.8	0.65	0.57	0.66	0.61	0.54

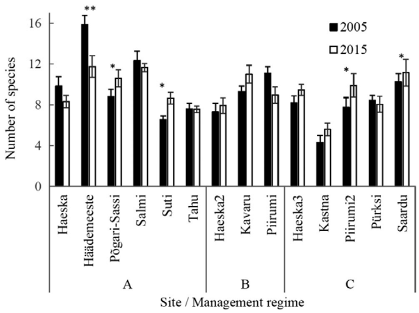

Figure 2. Average number of plant species per plot in the studied meadows with different management statuses A, B, and C (permanently managed, restored before and after 2005, respectively) in 2005 and 2015. Error bars represent ±SE (n = 20). Differences in the same area between years were detected with the SAS GLM LSMeans test (**$p < 0.001$ or *$p < 0.01$).

differences were detected with an LSMeans test. If the covariation was statistically significant, we included a new variable, community characteristic*year. In all analyses, the confidence level was set at 95%. In the multivariate dataset, the development of each site from 2005 to 2015 was visualized with PCA of the SAS PRINCOMP procedure. To identify the indicator plant species for each management group (permanently managed, restored before and after 2005), the R IndVal package (Dufrêne–Legendre indicator species analysis) was used (Dufrêne & Legendre 1997).

Results

Species Richness

The vegetation parameters and changes over 10 years of management are presented in Table 1. In 2005, the number of species per plot in abandoned meadows was significantly lower (7.8) than in meadows that were restored before 2005 (10.2) and in permanently managed meadows (9.2). Over 5–10 years of restoration between 2005 and 2015, the number of species per plot was adjusted and there was no significant difference between management groups. The same pattern was observed with the Shannon E index. The average number of species per m^2 increased in most meadows but declined in meadows that were permanently managed (Fig. 2), which could be explained by the different management histories of meadows (Fig. S1). Meadows that were historically mown had a significantly higher number of species.

The Shannon E index almost reached its maximum level by 2015 in meadows that had been restored both before and after 2005 (Fig. S2). The Shannon E values for permanent meadows were similar in 2005 and 2015. The values for both groups of restored meadows became closer to those of permanent meadows by 2015, but they were still similar to the 2005 results for meadows restored before 2005.

Plant coverage (Fig. S3) changed over 10 years in different ways in different management groups. For permanently managed meadows, coverage increased to 60–70%. Areas with recent

Table 2. Indicator species of permanently managed meadows in 2005 and 2015 and in meadows, qualifying as "favorable" by visual estimation (see Table S1 for qualifications).

Permanently Managed (2005)			*Permanently Managed (2015)*			*Favorable (2015)*		
Species	*Indicator value*	*pvalue*	*Species*	*Indicator value*	*pvalue*	*Species*	*Indicator Value*	*p-value*
Plantago maritima	0.808	0.001	*Glaux maritima*	0.603	0.001	*Potentilla anserina*	0.663	0.003
Juncus gerardii	0.771	0.001	*P. maritima*	0.597	0.001	*J. gerardii*	0.631	0.004
G. maritima	0.727	0.001	*P. anserina*	0.585	0.001	*Agrostis stolonifera*	0.605	0.027
P. anserina	0.635	0.001	*J. gerardii*	0.576	0.001	*Leontodon autumnalis*	0.59	0.001
Festuca rubra	0.621	0.001	*L. autumnalis*	0.545	0.001	*G. maritima*	0.588	0.004
Odontites vulgaris	0.532	0.001	*F. rubra*	0.53	0.003	*P. maritima*	0.587	0.001
L. autumnalis	0.497	0.001	*Lotus corniculatus*	0.483	0.001	*Eleocharis uniglumis*	0.556	0.002
Tetragonobolus maritimus	0.453	0.001	*Carex panicea*	0.482	0.001	*F. rubra*	0.549	0.034
Trifolium repens	0.386	0.002	*E. uniglumis*	0.455	0.006	*C. panicea*	0.476	0.027
Deschampsia cespitosa	0.37	0.002	*Trifolium fragiferum*	0.422	0.001	*T. fragiferum*	0.469	0.008
Trifolium pratense	0.357	0.002	*T. repens*	0.421	0.002	*L. corniculatus*	0.417	0.016
T. fragiferum	0.354	0.001	*Centaurium littorale*	0.414	0.001	*C. littorale*	0.412	0.017
Ranunculus acris	0.337	0.001	*Sagina nodosa*	0.304	0.002	*Trifolium repens*	0.408	0.024
Rumex acetosa	0.319	0.004	*Geranium palustre*	0.269	0.033			
Odontites litoralis	0.267	0.004	*D. cespitosa*	0.266	0.017			
Centaurium pulchellum	0.242	0.004	*Medicago lupulina*	0.225	0.025			
Potentilla erecta	0.242	0.011	*Rhinanthus serotinus*	0.225	0.021			
Succisa pratensis	0.242	0.009	*Galium uliginosum*	0.223	0.035			
Viola tricolor	0.242	0.01	*Linum cathatricum*	0.205	0.032			
Dantonia decumbens	0.224	0.015						

Table 3. Relations between *Phragmites australis* coverage and different vegetation parameters according to a SAS GLM linear regression model.

Vegetation Parameter	*DF*	*Type III SS*	*Mean Square*	F *Value*	*Pr* > F
Ratio of light-demanding plants	1	10.852	10.852	249.72	<0.0001
Average coverage (%)	1	78.647	78.647	0.23	0.6284
Ratio of wintergreen plants	1	1.177	1.177	14.26	0.0002
Ratio of moderately salt-tolerant plants	1	0.085	0.085	9.58	0.0021
Ratio of salt-tolerant plants	1	3.787	3.787	56.39	<0.0001
Ratio of humidity-tolerant plants	1	8.229	8.229	148.11	<0.0001
Ratio of water plants	1	18.889	18.889	644.75	<0.0001

restoration activities in 2005 and 2015 had coverage of less than 60%. In 2005, the areas restored after 2005 were abandoned reedbeds. Meadows restored before 2005 had recovered from active intervention over 10 years of management and reached coverage of over 60%.

The average and maximum vegetation heights increased in permanently managed meadows and meadows that had been restored before 2005 and decreased in meadows restored after 2005 (Fig. S4). The coverage of low-lying plants decreased in permanent meadows but remained the same in plots restored both before and after 2005. The coverage of medium-height plants increased in permanent meadows and meadows restored after 2005 but decreased in meadows restored before 2005.

IndVal analysis revealed that there were nine plant species that occurred only in permanently managed meadows in both 2005 and 2015 (Table 2). Altogether, 13 species served as indicators of meadows that were visually estimated as in favorable condition. Among these, eight species were found in permanently managed meadows in both 2005 and 2015, and four were found in permanently managed meadows only in 2015. Meadows restored before 2005 did not show such homogeneity (Table S2), but meadows restored after 2005 as well as those estimated as extremely poor included *Phragmites australis* and *Atriplex calotheca* as indicators in both years (Table S2).

Phragmites australis Coverage

The coverage of *P. australis* had a great influence on most vegetation parameters (Table 3). Its disappearance led to the appearance of plants with high light requirements (Fig. S5), water tolerance (Fig. S6A & S6B), and salt tolerance (Fig. S7A & S7B). The only factor that did not depend on *P. australis* coverage was average plant coverage.

Restoration and Management Effects

In a graph of the PCA results (Fig. 3), the first PCA axis describes 44.81% of the relation between the qualities of favorable and poor

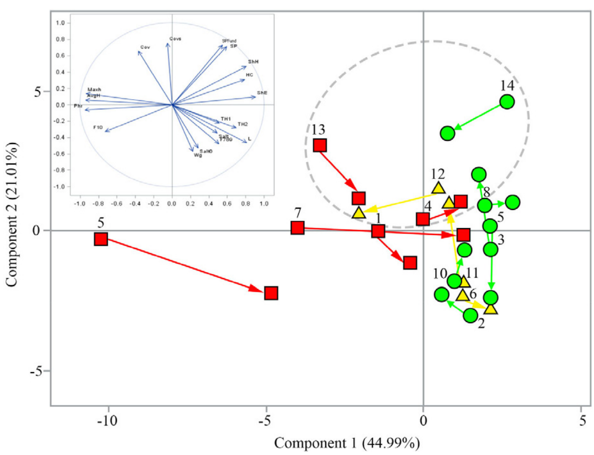

Figure 3. Dynamics of site development according to PCA (A) with a component pattern (B) by area from 2005 to 2015. The eigenvectors and their abbreviations are presented in Table S3. Green dots indicate permanently managed meadows, yellow dots indicate meadows restored before 2005, and red dots indicate meadows restored after 2005. The closed circle with a dotted line indicates which meadows were historically mown.

meadows. The Shannon E index, light-demanding plant coverage, and Shannon H index are on the positive end, and the average and maximum height of vegetation and coverage of *P. australis* are on the negative end. The second PCA axis describes 21.01% of the coverage, species pool, and number of species on the positive end as well as the coverage of wintergreen plants and moderately salt-tolerant plants on the negative end.

Discussion

Vegetation Parameters

To measure the effects of restoration on the vegetation in coastal meadows, we examined six permanently managed meadows (which were used as reference sites), three sites with a restoration history of at least 16 years (i.e. restored before 2005), and five sites with a restoration history of 5–10 years (i.e. restored after 2005). In 2015, all 14 meadows were managed under the EU agri-environmental scheme as permanent grasslands, which means they have undergone a 3-year restoration phase and are regarded as restored according to Estonian conservation practice. We measured changes in vegetation and compared them to the reference sites in 2005 and 2015 to determine whether the restored meadows (restored either before or after 2005) achieved similar vegetation parameters to the permanent meadows, which were managed without major interruption for centuries.

Our study outlined that specific indicators can be used to measure the quality of coastal meadow vegetation. The best quality indicators for coastal meadows are the coverage ratio of low-lying plants (more than 25%) and the proportion of these species (more than 23%) compared to species pool. The ratios of medium-height plants (over 40%), light-demanding plants (more than 60%), salt-tolerant plants, hemicryptophytes, and cryptophytes (more than 60%), and wintergreen plants (more than 65%) in relation to overall plant coverage were also considered to be good indicators of the quality of coastal meadows, in line with Pätsch et al. (2019). These plants take time to appear during the restoration process (Waldén et al. 2017), regardless of whether the degradation is characterized by tall herbs (Pakeman et al. 2017). Therefore, the main determinants of restoration success in our study were the replacement of *P. australis* and other water plants (EIV F10) by low-lying or medium-height, wintergreen, salt-tolerant, and light-demanding species.

It is acknowledged that mowing adds to species richness in many cases of seminatural grassland management (Tälle et al. 2016). This notion was supported by our research; historically mown meadows had more species than historically grazed meadow parts. Often, the appearance of specific species or species richness are used as indicators of the restoration of seminatural grasslands (e.g. Lindborg & Eriksson 2004; Lundberg et al. 2017), although changes in the number of species cannot always be a restoration target (Bakker et al. 2000). Our research revealed that, in coastal meadows, species richness may not be the main indicator of quality, as there is high diversity in the plant communities, associations, and types that comprise coastal meadows due to variations in location around the Baltic Sea, bedrock, salinity, inundation, and other factors (Pätsch et al. 2019). Some associations are more species-rich, and others are species-poor. Therefore, our research suggests that evenness is a better indicator of the quality of vegetation in coastal meadows than species richness. As expected, permanent meadows showed high evenness, while during restoration activities, the vegetation may include species from abandoned communities as well as recolonizing meadow plants. As a result, the E index may be lower for meadows being restored.

The plant coverage in well maintained meadows is 60–70%. During restoration, coverage declines since reedbeds (100% coverage) are suppressed and time is required for the recolonizing species to form a permanent grass mat, as reported by Berg et al. (2011). In our research areas, we observed that coverage stabilized over 10–16 years of restoration.

Phragmites australis Coverage

In recent decades, the common reed has become a serious conservation problem because it has spread into ecologically valuable habitats and, as it is a strong competitor, it has eliminated most other species (Roosaluste 2007). Thus, suppression of reedbeds is crucial during coastal meadow restoration (Sammul et al. 2012). Our results confirm that by decreasing the amount of reed, the ratio of light-demanding, wintergreen, salt-tolerant, and water-tolerant plants will increase significantly in 10–15 years. Currently, the height and presence of *P. australis* are used as indicators for quality estimations of coastal meadows under agri-environmental schemes that provide management subsidies. According to such schemes, reed stalks should be less than 50 cm tall (Lotman 2011). However, the abundance of reed is not mentioned in management regulations. Our results showed that, in permanently managed meadows, reed comprised less than 2% of the vegetation coverage, while in meadows that have been restored from abandonment for 5, 10, or 16 years, reed comprised more than 2% of the vegetation coverage. The proportion decreases over time, but even meadows with a 16-year restoration history did not reach the threshold of 2% *P. australis* coverage. Therefore, our study revealed that the abundance (and not only the height) of *P. australis* could be a good indicator of restoration success, and all measures to suppress reed while restoring coastal meadows from abandonment should be supported. According to interviews with land managers, many methods have been used to suppress reed and shrubs during early phase of restoration, such as burning reedbeds, mulching, and cutting combined with grazing. Additionally, Roosaluste (2007) indicated that the competitive ability of common reed could be decreased through shading by other plant species, severe frosts in winter, serious drought during the vegetative period, strong wave and ice activity on the shore, grazing, mowing, and burning. The mowing and burning techniques are described in detail by Huhta (2007).

Restoration and Management Effects

Actions taken to restore grasslands have usually been intended to return to the past and achieve historical fidelity. Thus, prior studies examining such areas have used evaluation criteria such as structural replication, functional success, and durability (Baker & Eckerberg 2016). However, in our experiment, we examined postabandonment restoration and tried to avoid a pre-abandonment focus (Valkó et al. 2016) by comparing our results to permanent meadows as reference areas that are undergoing environmental changes. During the 10-year experiment period, the vegetation parameters of all the reference meadows stayed within a similar range, with some minor changes (e.g. increase or decrease in species richness, vegetation height, and functional traits). Meadows restored after 2005 showed a significant quality improvement, and two of the three meadows in which restoration began before 2005 had reached the quality of permanent meadows, according to visual estimations during fieldwork as well as statistical analysis and IndVal analysis. Therefore, similar to papers on other types of grasslands (see, e.g. Lundberg et al. 2017), our study confirms that a 10-year restoration process is not enough to meet the ecological parameters of reference areas; at least 15 years of restoration are needed.

Estonian legislation and management planning documents (Lotman 2011) state that coastal meadows can receive restoration support and subsidies from the national budget for about 3 years, during which time restoration is expected. Then, these areas must enter the EU agri-environmental scheme, and management will be evaluated by the same criteria as any other seminatural grassland. We believe that a 3-year period for restoration from long-term abandonment is not sufficient for an area to qualify as a permanent meadow, and if national budgets are not able to support restoration activities for longer, the EU agri-environmental scheme should establish a 3–5-year transformation period for meadows still undergoing restoration to allow for additional reed-suppressing activities, like mowing, mulching, and controlled burning. We also recommend viewing the criteria for evaluating the coastal meadows' quality as targets rather than means, in accordance with Bakker et al. (2000). Today, the evaluation of coastal meadow management is based on, e.g. hectares, animal units, and grazing time. The only vegetation-related target is the height of vegetation, and the main targets of financing projects are indicators at higher trophic levels, like amphibian and bird species (Rannap et al. 2017). Our study suggests some measurable vegetation quality targets, which are totally missing in current conservation practice, for evaluation of coastal meadow restoration. We claim that the coastal meadows which have undergone the restoration process from abandonment can be considered as restored by vegetation quality and in favorable conservation status only after at least a 10-year constant management period with suitable grazing pressure. The removal of secondary vegetation, such as reed and shrubs in first phase, does not make a coastal meadow "restored," it needs time and effort to establish characteristic vegetation.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Number of species in historically mainly grazed (n = 200) and mainly mown (n = 80) meadow plots in 2005 and 2015.
Figure S2. The Shannon E index for different management groups and years.
Figure S3. Plant cover (%) in different management groups and years error bars represent ± SE.
Figure S4. Changes in the maximum and average measured vegetation height from 2005 to 2015 by management group.
Figure S5. Relation between *Phragmites australis* coverage and the ratio of plants with high light requirements (trendlines are illustrative only).
Figure S6. Relation between *Phragmites australis* coverage and the ratio of water-tolerant (A) and water plants (B) (trendlines are illustrative only).
Figure S7. Relation between *Phragmites australis* coverage and the ratio of moderately (A) and highly salt-tolerant (B) plants (trendlines are illustrative only).
Figure S8. The photos of studied coastal meadow sites.
Table S1. The main characteristics of the study sites in 2005 and 2015.
Table S2. Indicator species of meadows restored before 2005 and after 2005 in years 2005 and 2015.
Table S3. Eigenvectors for PCA.

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Original Research Article

Long-term effect of different management regimes on the survival and population structure of *Gladiolus imbricatus* in Estonian coastal meadows

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A B S T R A C T

Questions: How does the population structure of the threatened plant species *Gladiolus imbricatus* differ in the early and late stages of habitat restoration under different management regimes? What is the best management regime for the species?

Location: Luitemaa Nature Reserve in Southwest Estonia.

Methods: A long-term field experiment (2002–2004 and 2014–2016) studied the effect of four management regimes: (1) mowing in late July, (2) grazing by cattle, (3) grazing by sheep and (4) continuous lack of management (i.e. the control).

Results: In contrast to the highly positive short-term response to habitat restoration, in the long term, late-season mowing was the most favourable management type for *G. imbricatus*. The universal increase in juveniles across treatments during the early phase of the restoration project remained high only in mown plots. For the other treatments, after 10 years, the number of juveniles declined to the starting level or lower. Additionally, in contrast to the uniformly high number of premature and generative plants across treatments during the first two years of restoration, the number of premature plants in grazed sites declined. In particular, the frequency of premature and generative plants differed between the mowing and sheep grazing treatments in the long term. The success of generative reproduction was poor in the sheep-managed pasture, as all the shoots were grazed and none had any fruits or flowers.

Conclusions: While grazing is the most commonly subsidised restoration measure applied to coastal meadows, we recommend diversification of management types by promoting late-season mowing and reducing grazing intensity. In particular, sheep grazing must be avoided. The results of short-term evaluation of restoration methods can be misleading, and long-term monitoring must be a default evaluation task in biodiversity management support schemes.

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1. Introduction

Most vegetation in Europe evolved under the constant influence of man. Species-rich grasslands are semi-natural heritage communities that developed under long-term traditional mowing and grazing (Austrheim et al., 1998; Eriksson et al., 2002; Joyce, 2014; Kull and Zobel, 1991) However, cessation of traditional land use measures (Kahmen and Poschlod, 2004; Pykälä et al., 2005; Valkó et al., 2018), intensified grazing (Bouchard et al., 2003; Dupré and Diekmann, 2009; Rosen, 1982) and fertilising (Jacquemyn et al., 2003; Myklestad and Sætersdal, 2004; Spiegelberger et al., 2006) have reduced the species richness of plant communities (Joyce, 2014) and diminished the provision of grassland-specific ecosystem services (Wehn et al., 2018b). This dramatic decline in semi-natural species-rich grasslands in Europe and the loss of habitat connectivity for the species that rely on these habitats have resulted in the extinction of local species (Harrison and Bruna, 1999; Waldén et al., 2017), thereby causing a decline in biodiversity at different trophic levels of semi-natural communities (Krauss et al., 2010).

Grassland abandonment, as a conservational problem, can be addressed as an opportunity for restoration (Valkó et al., 2016), but this leads to numerous challenges. Numerous authors have outlined that species diversity in heritage communities significantly depends on the management history—that is, the historical context—of the site (Gustavsson et al., 2011; Otsus et al., 2014; Purschke et al., 2014). This is also referred to as traditional ecological knowledge (Wehn et al., 2018b). Those aiming to conserve and perform restoration management for semi-natural communities must identify methods and economically viable practices that are appropriate for those activities (Rannap et al., 2017; Tälle et al., 2016; Valkó et al., 2018). Although the reintroduction of traditional management regimes is most appropriate for grassland restoration from an ecological perspective, it is not feasible in most cases (Valkó et al., 2018). Numerous authors have experimented to find contemporary replacements for traditional land use, evaluating their ecological and economical trade-offs (Bonari et al., 2017; Henning et al., 2017; Liira et al., 2009; Szépligeti et al., 2018). A meta-analysis of various experiments on benefits of grassland management by either grazing or mowing for biodiversity revealed that grazing has a more positive effect than mowing (Tälle et al., 2016). However, another meta-analysis of meadow mowing regimes indicated that the most effective mowing frequency depends on the productivity of the given site, but in general, less frequent mowing regimes yield better results for biodiversity (Tälle et al., 2018).

The effects of different herbivore species and breed-grazing strategies on grassland biodiversity were thoroughly analysed by Metera et al. (2010). The authors conclude that grazing species have different food preferences and suggest that mixed grazing systems may be a way to guarantee diversity and that local conditions should be considered instead of using blanket stocking rates, as suggested by agri-environment schemes (Metera et al., 2010). Different restoration experiments compared the re-introduction and replacement of old breeds by allowing sheep, goats (Benthien et al., 2018, 2016), cattle (Lyons et al., 2017; Oldén et al., 2016; Schaich et al., 2010) and horses (Köhler et al., 2016) to graze. These efforts yielded the expected results in terms of restoration. In Europe, it is a common practice to replace milk cattle with beef cattle, both equally contributed to semi-natural grassland management and restoration activities (Laurila et al., 2015).

Numerous works on bird and arthropod species have examined different management and restoration activities in wet and coastal meadows (Bruppacher et al., 2016; O'Neill et al., 2003; Verhulst et al., 2011). Compared to studies of animals, however, long-term and large-scale demographic studies of plants are scarce. A 32-year study of *Ophrys sphegoides* indicated that sheep grazing is more favourable for the species than cattle grazing (Hutchings, 2010), however, the study indicated that over half of the plants were browsed by livestock. Schrautzer et al., 2011Schrautzer et al., (2011) reported that mowing had a positive effect on *Dactylorhiza incarnata* populations, as there was an exponential increase in the number of flowering plants during the first 10 years of the experiment. Further, Lundberg et al. (2017) reported that several protected species in Norwegian dry coastal dunes had a positive reaction to mowing only after 10 years of annual efforts.

The coastal meadow restoration efforts in the Luitemaa Nature Reserve are not focused on maintaining the *G. imbricatus* population in particular, but on creating a habitat for rare shorebirds and natterjack toads. Our grassland management experiment studied a very important side effect of the grassland restoration process: the response of a rare grassland species to various types of maintenance. Since we have already observed the positive reaction of *G. imbricatus* to restoration activities during the first three years of management and its uniform reaction to all management types (Moora et al., 2007), here we examine whether the trend continues in the long term. We hypothesise that different management regimes have different effects on the structure of the *G. imbricatus* population and its survival during long-term restoration efforts.

2. Materials and methods

2.1. Study species

The sword lily *Gladiolus imbricatus (Iridaceae)* is a decorative tuberous clonal plant that is native to Central and Eastern Europe, the Mediterranean, Caucasia and West Siberia (Meusel et al., 1965). *G. imbricatus* grows up to 30–80(100) cm tall, and it forms bulb-like tubers that are 1–2 cm in length and tubercules for vegetative reproduction. Vegetative plants start as a single-leaf juveniles and then grow to become two-leaved premature plants. Generative plants have single slender stalks with 2 rosette leaves and 1–3 leaves on the flower stalk and 3–10 purple flowers within a one-sided inflorescence. In Estonia, flowering occurs in July, and relatively large seeds (1.8 mg) ripen during the first half of August. One plant can produce 200–400 seeds, and a chilling period of several months is needed for the seeds to germinate when temperatures increase in late spring (Rakosy-Tican et al., 2012). Prior studies reported that the success of establishment in reintroduction field experiments can range from 60% (mowing and mulching) to 20% (burning and no management; Jõgar and Moora, 2008). Reaching the generative stage is rare and may be time-consuming. Seeds can survive in a seed bank, but the success of establishment after storage in a seed bank depends on the height of vegetation, availability of light and level of nearby disturbance. Significantly higher seed germination can be achieved by removing litter, bryophytes and the above-ground parts of plants; ensuring the availability of larger gaps in vegetation; and planting in open meadows (as compared to shaded areas covered by large tussock grasses and overgrown with willows; Kostrakiewicz-Gierałt, 2014a).

No specific literature is available on *G. imbricatus* dormancy patterns, but in their review of dormancy among perennial herbaceous plants Shefferson et al., 2018 Shefferson et al., (2018) found that rhizomatous species have the longest maximum dormancy values, while those with corms or bulbs have the shortest. In our special study, we observed only some hypogeal germination and no dormant bulbs (personal unpublished observation). *G. imbricatus* is plastic in its responses to the environment, as its productivity and traits depend on the light conditions and vegetation density.

The *G. imbricatus* species is categorised as threatened, red-listed or under protection across Europe (Kostrakiewicz-Gieralt et al., 2018) and has become locally extinct in numerous regions (Richter, 2012). In Estonia, *G. imbricatus* is under legal protection and is considered to be vulnerable (Kull et al., 2018), as its population is in decline (Kukk and Kull, 2005). *G. imbricatus* occurs in various habitats across Europe, from termophilous oak forests to wet meadows, including floodplains, coastal grasslands and marshes Kostrakiewicz-Gieralt, 2014b(Kostrakiewicz-Gieralt et al., 2018). In Estonia, the distribution of the species is restricted to a sub-region of Livland (the southern half of Estonia), forming a west–east belt from coastal meadows in the west to flooded meadows near the River Emajõgi in the east (Kukk and Kull, 2005). The species is threatened by the picking of flowering plants and changes in land use (i.e. abandonment and urbanisation of coastal areas). During the previous century, the abandonment of seashore and floodplain grasslands resulted in the encroachment of reeds and bushes. Grazing, which is the most traditional measure of grassland restoration, is unadvisable for the species (Krall et al., 2010; Richter, 2012). Thus, reintroduction has been recommended (Jõgar and Moora, 2008).

2.2. The research area and description of the management experiment

In the restoration management planning and EU agri-environmental schemes, coastal grasslands are intended to be maintained as low-sward homogeneous permanent grasslands. Many grasslands managers use the opportunity for a short term contract for habitat restoration to begin with, but are then required to switch to the contract system of agri-environmental schemes. Grazing is the prescribed as the main management method by the agri-environmental support scheme, while restoration support schemes additionally allow the use of mowing, mulching and other methods as well. Grazing with different beef cattle is the main method of conservation management in coastal grasslands in Estonia. Sheep (mostly meat breeds) do not frequently graze in coastal grasslands due to wet conditions and numerous specific diseases. Moreover, large carnivores have become a threat to sheep as their populations have increased.

The research area is located in the Luitemaa Nature Reserve on the southwestern coast of Estonia (hereafter, Luitemaa; Fig. 1A, B, C). Luitemaa hosts approximately 800 ha of an EU priority habitat called the Boreal Baltic coastal meadow (92/43/EEC), which represents approximately 10% of the current area of this type of habitat in the country. The area is edaphically homogeneous and was established on an area that used to be at the bottom of the sea due to the post-glacial land uplift (0.1 mm per year). The sandy loam is covered by a humus layer 10–20 cm deep.

The plant community in the experimental sites belongs to the association of the *Deschampsio-caricetum nigrae* type (Krall et al., 1980), which is typical of coastal areas in Estonia. The prevailing species in the community are *Molinia caerulea* and *Sesleria caerulea*, with *Festuca rubra* occasionally co-dominating in more grazed areas. Historically, the lower parts of the meadow (i.e. those near the shoreline) have been used for grazing by a variety of domestic animals, including dairy cows, heifers, sheep and horses.

Historically, the lower part was separated from the higher parts of the meadow by different types of fences or was guarded by shepherds. The higher parts of the meadow were used for haymaking and late-summer grazing (Kasvandik et al., 2003). This management regime declined in the 1950s, and the entire area was abandoned from the 1970s to the 1990s (personal communications). All the experimental plots are situated in the upper zone of the meadow (0.5–1 m above sea level), which was mown and grazed in history (Fig. 1B). However, these upper areas continue to be flooded by brackish seawater, with floods ranging in frequency from once to several times a year.

In 2001, an intensive habitat restoration project focusing on rare birds and natterjack toads was commenced in the Boreal Baltic coastal meadow (1630*, Natura, 2000) with the support of the EU LIFE Nature programme (Kose et al., 2004). The restoration and management activities have continued and been extended by EUagri-environmental support and various other projects until the present. Farmers in this area chose different types of livestock for the restoration activities and introduced new adaptive management patterns in different parts of Luitemaa.

2.3. Experiment description and sampling

In 2002, within abandoned grasslands of the upper part of the coastal meadow, we identified distinct areas in which *G. imbricatus* populations had survived and specimens were abundant enough for analytical experiments (for details, see Moora et al., 2007). These locations were very scarce and scattered along 7 km of the coastline. We selected four different management regimes: 1) grazing by beef cattle, 2) grazing by sheep, 3) late July mowing and 4) the continuation of abandonment

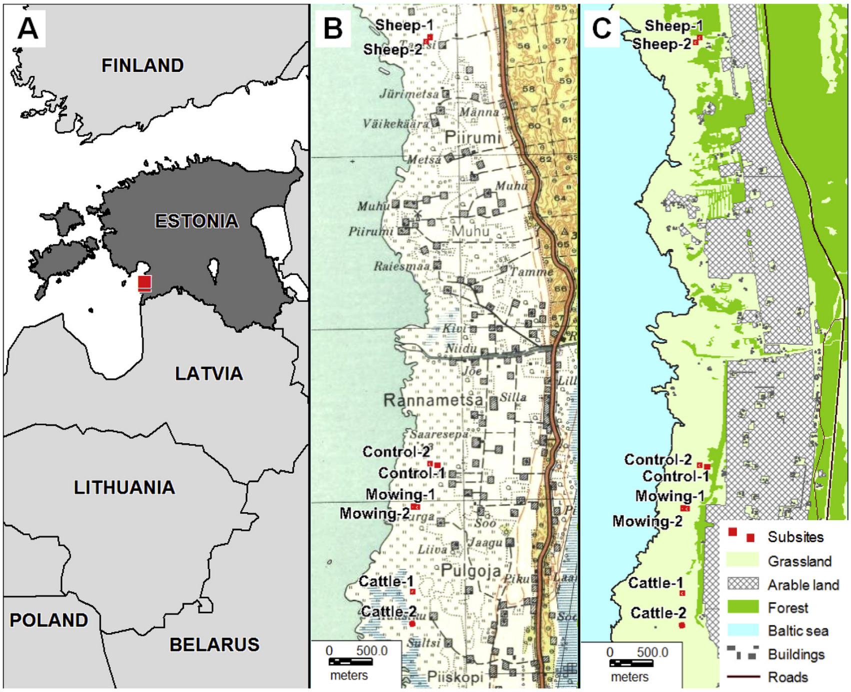

Fig. 1. The location at which *G. imbricatus* was researched in the Luitemaa Nature Reserve in southwestern Estonia (A). The distribution of study sites on a map from 1938 (B) and a contemporary land use map (C). Source for maps: the WMS-service of the Estonian Land Board.

(as the control). Each treatment was repeated at two subsites within a larger site given the same treatment. The treatments were partly spatially clustered because of the scarcity of *G. imbricatus* populations and the low management stability of the land owners at that time. The clustering, however, probably has only some negative effects on the representativeness of the study, as (1) the base environmental conditions are similar throughout the coastline examined in the experiment and, (2) after some years, management intensity became different between subsites given the same treatment because of heterogeneous behaviour of grazing animals.

The grass is mown after the 15th of July each year, dried and then collected. Thereafter, the areas are exposed to occasional grazing by beef cattle as part of a larger paddock. Grazing in both treatments was not intensive as legislation has set the limit of average grazing pressure up to 0.8–1.2 livestock units (LU) per hectare throughout the vegetation period from early May until late September (Lotman, 2011). Further, a paddock system was utilised to regulate grazing intensity and guarantee food availability for livestock. All grazed and mown areas are fenced permanently year-round except the shoreline, where fences are removed in the winter for safety reasons. The abandoned portion of the meadow, which has remained unused since the 1980s, was used as the control for the current study. The abandoned areas are slowly becoming overgrown with *Alnus glutinosa*; *Salix ssp.*; and tall herbs such as *Filipendula ulmaria, Molinia caerulea, Carex disticha, Selinum carvifolia, Angelica palustris* and *Angelica archangelica*. During the research period, the control areas and nearby sites remained open.

In 2002, two 20 × 20 m subsites were randomly located within each site. Ten 1-square metre plots were randomly placed in these subsites each year. Within these plots, *G. imbricatus* specimens were counted at three ontogenetic stages: 1) juveniles (i.e. one-leaved seedlings and vegetative juveniles; Fig. 3), 2) premature plants (i.e. two-leaved or vegetative adults) and 3) generative (i.e. flowering) plants. The plant coverage, species composition (i.e. presence and cover), maximum height and upper height limit of leaves were reported for each plot. Measurement was done during the second half of July, when the plants were fully flowering and mowing had not yet begun. Sampling was performed annually from 2002 to 2004 and then the sample was re-surveyed annually from 2014 to 2016. From 2005 to 2013, no plants were measured, but coastal meadow management was performed in the same manner.

In the last years of the experiment, vegetation in the managed plots was lower than in the abandoned plots (Fig. 2). However, there are significant variations in treatments between years (Table A.2, Figs. A1 and A2). The maximum height of vegetation reflects the higher peaks of flowering shoots in the plots (Fig. 2A and A2). It varies significantly over time (Table A.2), although it is significantly higher in abandoned plots. The average height of vegetation and the upper height of leaves in

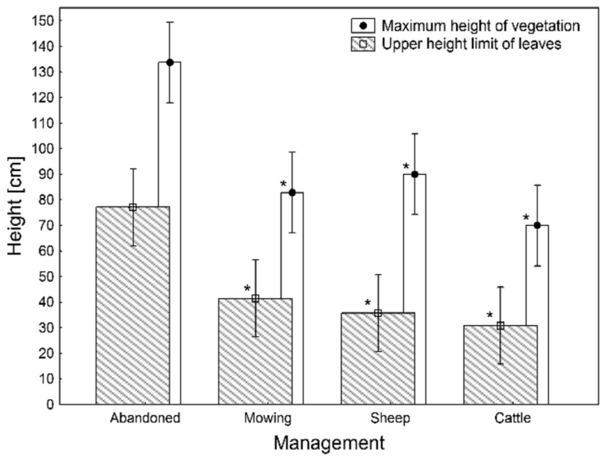

Fig. 2. Mean vegetation height over three years under four types of management (more details in Table A.2 Fig. A1). Whiskers denote a 95% confidence interval of means. Asterisks denote significant differences from the abandonment treatment according to Tukey post-hoc multiple pair-wise comparison tests.

Fig. 3. Juvenile and premature stages of *G. imbricatus*. The one-leaf stages formed a pooled group of juveniles (I A: seedlings; I B: one year or more, I C: two years or more) and II represented two-leaved premature or vegetative adults. Photo by Märt Kose.

grassland plants follow the same pattern (Figs. 2 and A1). Additionally, the plots grazed by sheep and cattle have significantly lower average vegetation than abandoned areas (Table A.2). The species richness of plots also contrasted between treatments (Table A.2, Fig. A3). Specifically, the abandoned subsites had the lowest species richness and the mown subsites had the highest species richness.

In 2016, an additional study was carried out. Some parameters of *G. imbricatus* specimens were measured for comparison with the vegetation parameters (i.e. height of rosette leaves, number of flowers). Up to 20 specimens were collected per treatment when the number of specimens within the given age group was available (Fig. 5).

In 2019, juvenile and premature plants were excavated from three 20×20 cm plots for each treatment to estimate the potential age of plants according to the morphology of bulbs/tubers. One-leaved specimens were distributed quite evenly in terms of the three developmental stages of tubers: seedlings, second-year plants and older plants (Fig. A4, Table A.3). One-leaved *G. imbricatus* specimens were all regarded as juveniles, even though they were different ages (Fig. 3). The proportion of juveniles of each bulb stage was similar for all treatments (Fig. A4, Table A.3).

2.4. Data analysis

Plot-level data were pooled at the subsite level, as sampling plots were located randomly within the subsite each year. The effect of treatments, successive years, ontogenetic stages and their interactions were evaluated based on the log-transformed count of individuals and a general linear mixed model. In the model, subplots were defined as random factors. The post-hoc pair-wise differences among specific management regimes were estimated using the Tukey HSD multiple comparison test. Another analogously structured model was run using logit-transformed frequency data regarding the ontogenetic stages of specimens in various plots within a subsite. The SAS 9.3 MIXED procedure was used for both analyses (SAS Institute Inc.). The model-based least-square means were back-transformed to real-life estimates, with 95% confidence interval ranges.

3. Results

3.1. Population number and structure

The mixed model results show very complex dynamics in terms of population size (Table 1). *G. imbricatus* juveniles increased in number during the starting phase of the restoration project for all treatments, particularly in mown plots (Fig. 4A). The abundance of juveniles in mown areas remained relatively high in the long term, even though the numbers reported from 2014 to 2016 were slightly lower than the peak observed in the third year of the experiment. For the other treatments, however, after 10 years, the number of juveniles declined to the starting level or below. This was the case for the unmanaged areas in 2015 and the sheep management plots in 2016 (Fig. 4A).

Further, the abundance of vegetative and generative shoots did not vary significantly between the treatments during the first two years of restoration (i.e. 2002 and 2003; Fig. 4B–C). However, in 2004, the number of premature shoots had declined in grazed plots and differed significantly from the estimates in the mown areas. Moreover, the numbers of premature and generative specimens were not statistically different from the numbers in the starting year across treatments, even though they did decrease under both grazing treatments. The unmanaged plots showed the most stable populations of premature and generative specimens.

The generative reproduction in the sheep-managed pasture was very poor (Fig. 5), as all the shoots were bitten and none had flowers or fruits (Table A.4, Fig. A5). In 2016, the height of *G. imbricatus* vegetative leaves (i.e. rosette leaves) was comparatively measured and found to be significantly higher during all ontogenetic stages in abandoned plots than in plots given other treatments (Fig. 5, Table A1). The leaf height of juveniles corresponds to the upper height of leaves of grasses in the plots (Fig. 2).

Table 1
Results of the mixed models in terms of the abundance and frequency of *G. imbricatus* at the subsites.

Effect	Abundance (log-transformed)			Frequency (logit-transformed)		
	df	F-statistic	P	df	F-statistic	P
Treatment	3;1120	19.78	<0.0001	3;40	11.82	<0.0001
Stage	2;1120	224.81	<0.0001	2; 40	55.07	<0.0001
Treatment*Stage	6;1120	5.90	<0.0001	6; 40	9.31	<0.0001
Year	4;20	5.30	0.0045	4; 20	3.44	0.0271
Treatment*Year	12;1120	3.04	0.0003	12; 40	3.40	0.0018
Stage*Year	8;1120	17.98	<0.0001	8;40	8.16	<0.0001
Treatment*Stage*Year	24;1120	1.16	0.267	24;40	1.98	0.0271
Covariance parameters	Estimate	Z-statistic	P	Estimate	Z-statistic	P
Random: SubSite(Treatment; Year)	0.012	2.170	0.015	0.0293	2.06	0.0197
Repeated: Year. Subject: SubSite(Treatment)	0.003	0.710	0.4771	0.0034	0.40	0.6917
Residual	0.112	0.005	<0.0001	0.0312	4.47	<0.0001

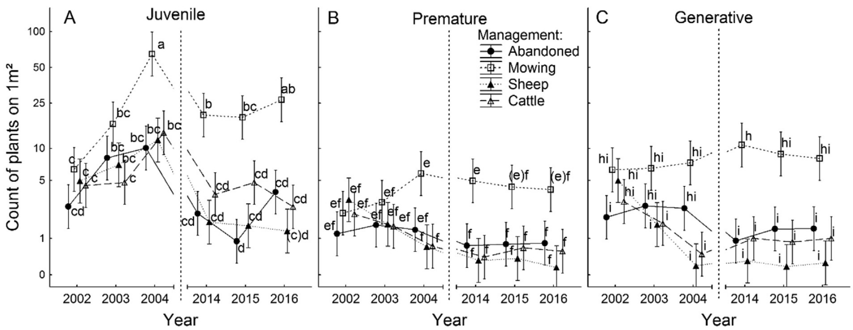

Fig. 4. Abundance response of *G. imbricatus* in different ontogenetic stages (i.e. juvenile, vegetative and generative) to different management regimes from 2002 to 2004 and 2014–2016. Y-axis is log-transformed, Statistically significant differences in abundance ($p < 0.05$) revealed by Tukey tests are indicated with different letters within the same age group. Whiskers denote a 95% confidence interval of means. Vertical dotted lines denote the survey gap from 2005 to 2013.

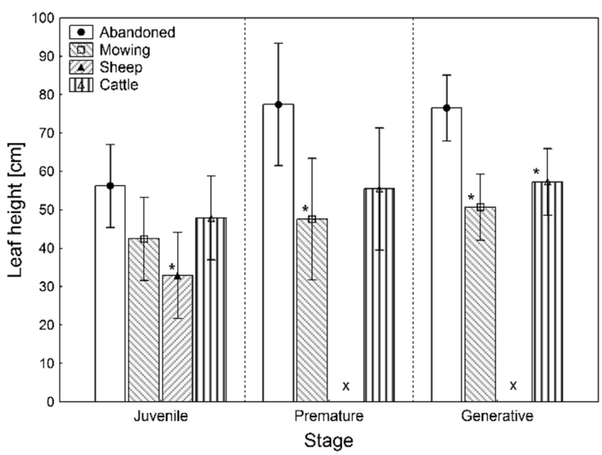

Fig. 5. The height of *G. imbricatus* vegetative leaves (i.e. rosette leaves; $n_{max} = 20$) during all ontogenetic stages in different management plots in 2016. Statistically significant differences in mean height between the abandoned treatment and other treatments revealing by Tukey multiple comparison tests are indicated by asterisks within the same age group. Whiskers denote a 95% confidence interval of means. X denotes missing ungrazed specimens in the given age group (only applicable to the sheep treatment).

The proportion of browsed *G. imbricatus* shoots of different ontogenetic stages in grazed plots differed significantly across years (Table A.4, Fig. A5). In 2014, the proportion of browsed shoots in all plots grazed by cattle was higher than that in sheep pastures, while in 2015 and 2016, the opposite was true. The average browsing rate of juveniles was 45–50% for cattle and 15–40% for sheep. The average browsing rate for generative shoots was 70–100% in both treatments. The most significant difference was observed in 2016 for browsing of premature shoots, with an average of 5% for sheep and almost 100% for cattle.

3.2. Population performance—frequency

There was a gradual decline in population frequency within the subsites (across 1×1 m plots) under all grazing treatments (Fig. 6, Table 1, right) as well as in abandoned plots in certain years. A particular difference in the occurrence frequency dynamics of premature and generative plants was observed between the mowing and sheep grazing treatments in the long

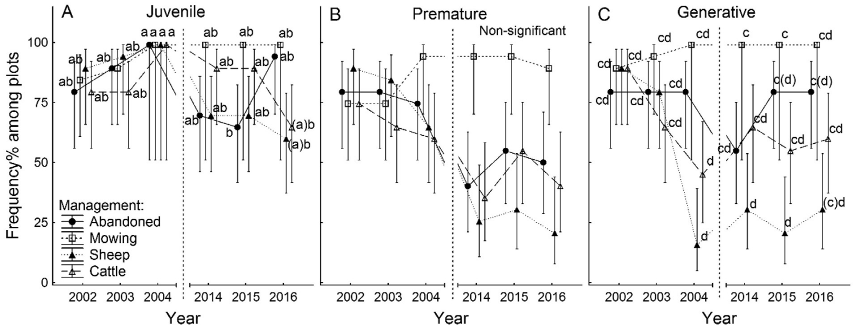

Fig. 6. Occurrence frequency (%) of *G. imbricatus* plants in plots under each management regime, presented by development stage (i.e. juvenile, premature and generative). Letters indicate the groups, which were significantly different ($p < 0.05$) according to the Tukey tests. Whiskers denote a 95% confidence interval of means. Vertical dotted lines denote the survey gap from 2005 to 2013.

term, although analogous trends were observed for juvenile plants (Fig. 6C). Less evident but similar trends were also observed for cattle grazing plots. The same trend was reported for premature plants, but the differences are not statistically significant (Fig. 6B).

4. Discussion

In 2002, when restoration activities began, all areas chosen for the experimental management regimes had a similar number and frequency of *G. imbricatus* specimens at each development stage. The mowing treatment resulted in a tenfold increase in the number of juveniles between 2002 and 2004, which was much more than the number reported in other years. The significant increase in the number of juveniles in mown plots in 2003 and 2004 may indicate that management disturbances had a positive effect on seed recruitment from the seed bank or new seeds from more abundant generative specimens. The increase was probably induced by the increased availability of establishment microsites and improved light conditions for germination, as reported by Kostrakiewicz-Gierałt (2014a) and Kostrakiewicz-Gieralt (2014b). The regeneration intensity in mown plots declined but stabilised after 10 years and was still at a higher level than before the restoration began. This short-term positive reaction was confirmed in an additional observation from nearby site in 2019, where long-term management of combined grazing and mowing led to the formation of tall-sedge areas with only a few *G. imbricatus* specimens, but the change in management to end-milling cutting in autumn 2018 led to a boost in juveniles (both, from bulbs and seedlings, as estimated from excavated specimens) and flowering shoots in 2019 (personal observation). An analogous short-term reaction of *G. imbricatus* to mowing was observed by (Kubíková and Zeidler, 2011) in the Na Bystrem meadow in Moravia.

The dynamics of premature and flowering shoots were different from those of juveniles. In abandoned areas and both types of grazed areas, the number of specimens of both stages began to decline after the second year of the experiment. By 2004, the frequency of flowering shoots decreased from almost 100% to 20% in the plots grazed by sheep. Further, in abandoned areas, the number of flowering individuals declined in a similar way to the grazing treatments, but the plants were more evenly distributed in the abandoned areas than in grazed areas. *G. imbricatus* is a phenotypically plastic plant, as it can adjust leaf length to rising competition with taller herb-layer vegetation during abandonment and in the early stage of encroachment of its habitats (Hänel and Müller, 2006; Kostrakiewicz-Gieralt, 2014b; Richter, 2012). Indeed, in the last year of the survey, the rosette leaves of generative *G. imbricatus* specimens were much taller in the long-term abandoned sites than in other treatments, indicating the plants' phenotypical plasticity to long-term encroachment. The average height of vegetation or the upper limit of leaves of vegetation was significantly lower in grazed plots. However, this was the case in all areas, indicating that the areas reflected annual environmental conditions in similar ways. The average height of the rosette leaves of *G. imbricatus* corresponds to the pattern of average grass leaf level across management regimes. The results confirm the conclusions of earlier studies regarding the abandonment effect on *G. imbricatus* (Hänel and Müller, 2006; Kostrakiewicz-Gieralt, 2014b; Kubíková and Zeidler, 2011; Richter, 2012): that plants become less abundant but flowering shoots elongate in response to competition for light and pollinators and, consequently, *G. imbricatus* populations survive meadow abandonment and overgrowth for a rather long time.

In contrast to positive trends in short-term counts, the re-survey of sites from 2012 to 2016 revealed that the population of *G. imbricatus* declined in grazed areas and continued to flourish only in mown plots. The contrast between the long-term and short-term observations supports the objective assessment, which suggested that the goals of ecological restoration can be achieved only after 10 years of treatment (Joyce, 2014; Koch et al., 2017; Lundberg et al., 2017). Lundberg et al. (2017) observed that, over 16 years of mowing treatment, the increase in the target species became significant only after year 10. These results warn against prematurely making conclusions regarding the degree of success in the early stages of restoration.

Different restoration measures applied to *G. imbricatus* led to different population performances after 15 years of management. Mowing is the most—and only truly—favourable management regime for *G. imbricatus*, as suggested by several other recent studies (Bonari et al., 2017; Tälle et al., 2018). However, mowing should be moved to later in the season, just after the ripening of seeds.

Neither grazing regime is favourable, as both showed a decline in population, particularly in the premature and flowering stages. Previous research indicates that sheep browse *Gladiolus* more selectively (61%) than cows (48% (Kose and Moora, 2004);). From 2014 to 2016, we observed that browsing habits differ annually, and while sheep browse almost half of the juveniles from the grass, the cows' browsing can vary yearly from 20 to 40%, although the availability of plants is similar. Two-leaved plants' leaves are more visible in grass and are browsed significantly more by sheep. Additionally, the flowering shoots are highly distinguishable from the rest of the grass and are eaten selectively by sheep. Yearly differences may indicate the heterogeneity of grazing patterns in different subsites (i.e. different paddocks), i.e. the patterns of animal behaviour may also affect the population and structure. For example, one of the cattle treatment sites, which was selected in 2002 and features the only population in a large area, has become a favourable resting place for animals. Plants almost disappeared from there, but a large number have spread to the surrounding 50 ha. Field observations indicated that after late grazing with sheep in 2003 and 2004, in the following years, a large number of *G. imbricatus* seedlings appeared near the paths of sheep and in their resting places. Similar zoochory was reported by land managers throughout the restoration period. The prescribed grazing pressure (0.8−1.2 LU/ha) was probably too high; Lyons et al. (2017) reported a long-term positive response to grazing pressure of 0.2 LU/ha in upland calcareous grasslands, although this is a habitat with much lower productivity. The low year-round horse grazing pressure (0.3 in the vegetation period and 0.2 in winter) was found to be favourable for rare species and communities in dry calcareous grasslands (Köhler et al., 2016) and are recommended for dry sandy grasslands (Henning et al., 2017). On the other hand, Tóth et al. (2018) suggest that livestock type is more crucial than grazing intensity in short-grass steppes and that sheep may be more selective grazers in cases of low grazing pressure (Tóth et al., 2018). This could be the case for *G. imbricatus*.

We suggest that management schemes that favour grassland biodiversity and rare plant species must consider the grazing habits of the available grazers, grazing pressure and timing. The diverse management patterns of grasslands have been suggested to be more effective for preserving arthropod diversity (Bucher et al., 2016), pollinators (Moroń et al., 2008; van Klink et al., 2016), amphibians and breeding birds and feeding migratory waders (Arbeiter et al., 2018; Rannap et al., 2017). This is probably important for plants. Small- and large-scale heterogeneity is characteristic of natural ecological conditions, which must be considered while planning optimal and effective restoration treatments (Valkó et al., 2018; Wehn et al., 2018a,b).

We showed that the short-term part of our experiment leaves an overly positive impression about the effectivity of restoration management support scheme (i.e. experiment within the time-frame of restoration support scheme), while the long-term continuation of the same management types shows their negative effect on population restoration of *G. imbricarus*. The latter negative results, however, are attributed to the following maintenance support by agri-environmental schemes (i.e. experiment within the time-frame of agri-environment scheme) after the maximum three year support for habitat restoration. Additionally, restoration contracts are more flexible when it comes to choice of management type than agri-environmental schemes. Specifically mowing is not a conventional measure for coastal meadows maintenance under the agri-environmental support schemes and its application needs special permits. Late-summer mowing (with mulching), however, is probably a more cost-effective on the upper parts of coastal meadows (Bonari et al., 2017; Henning et al., 2017; Liira et al., 2009; Szépligeti et al., 2018) and supports more efficiently certain rare plant species than prescribed grazing. There have been doubts about EU Common Agricultural Policy ability to support achieving the biodiversity targets (Pe'er et al., 2014). We suggest that the problem might start from inadequate restoration and management methods, but the short-term monitoring prescribed for restoration schemes is not able to detect these problems. We suggest that the most favourable management types for upper parts of coastal meadows is rotational treatment in which mowing, grazing and no management are applied in different years, which promotes seed ripening and distribution, creates various microsites and disturbances. Finally, as we observed the boosting reaction of *G.imbricatus* in the consequence of changed grazing-mowing management type to the late-summer end-milling cutting at the meadow neighbouring the experiment, litter-free ground in the spring can be an additional critical factor for *G. imbricatus*, however, these late-summer removal treatments should be tested and promoted in future.

5. Conclusions

Our study reveals that when coastal meadow restoration and maintenance managements target the general aims of agri-environmental schemes, such as the promotion of low-sward grassland and habitats for shoreline-breeding waders and migratory birds, while other more specific conservational aims may have been neglected. Therefore, restoration and agri-environmental management schemes need more precise multi-target planning, i.e. must consider all conservation values of the ecosystem. While grazing is the most common restoration and maintenance measure for coastal meadows, we recommend diversification of management types by promoting late-season mowing and reducing grazing intensity. Sheep grazing must be avoided or regulated to low intensity levels. The short-term evaluation results of restoration and management methods can be misleading, and the long-term multi-indicator monitoring of management contracts must be implemented.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00761.

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Appendices for "Long-term effect of different management regimes on the survival and population structure of *Gladiolus imbricatus* in Estonian coastal meadows"

Global Ecology and Conservation

Marika Kose, Jaan Liira, Kadri Tali

This PDF file includes:

Table A. 1. The results of mixed models about the effect of treatment on the leaf height of *G.imbricatus*.

Table A. 2. The results of mixed models about the differences of vegetation parameters between years and treatments.

Figure A. 1. The average height of the upper height of leaves the vegetation of survey plots.

Figure A. 2. The maximum height of vegetation in plots by year.

Figure A. 3. The species richness by year.

Table A. 3. The results of the mixed model about proportional distribution of one-leaved (juveniles) and two-leaved (premature) plants by bulb morphology.

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Table A. 4. The browsing proportions of *G. imbricatus* stages by year.

Figure A. 5. The browsing proportions of *G. imbricatus* stages by year.

Table A. 1. The results of mixed models about the effect of treatment on the leaf height of *G.imbricatus*.

	Juveniles			Premature			Generative		
Effect	df	F-statistic	P	df	F-statistic	P	df	F-statistic	P
Treatment	3;131	3.08	0.0296	2;108	3.72	0.027	2;107	9.6	0.0001
Covariance parameters	Estimate	Z-statistic	P	Estimate	Z-statistic	P	Estimate	Z-statistic	P
Random:									
SubSite(Treatment)	56.4	1.28	0.0996	123.5	1.18	0.12	32.5	1.05	0.1467
Residual	68.7	8.09	<0.0001	91.4	7.35	<0.0001	99.1	7.31	<0.0001

Table A. 2. The results of mixed models about the differences of vegetation parameters between years and treatments.

	Vegetation maximum height 2014-2016			Vegetation upper leaf layer height 2014-2016			Species richenss 2014-2016		
Effect	df	F-statistic	P	df	F-statistic	P	df	F-statistic	P
Treatment	3;224	11.95	<0.0001	3;224	7.59	<0.0001	3;4	154.09	0.0001
year	2;224	10.97	<0.0001	2;224	22.83	<0.0001	2;8	9.57	0.0075
Treatment*year	6;224	2.95	0.0086	6;224	2.76	0.013	6;8	4.9	0.0216
Covariance parameters	Estimate	Z-statistic	P	Estimate	Z-statistic	P	Estimate	Z-statistic	P
Random:									
SubSite(Treatment)	114.6	1.27	0.1027	105.9	1.29	0.099	-0.09	-0.26	0.797
Residual	402.0	10.58	<0.0001	308.0	10.58	<0.0001	17.73	10.58	<0.0001

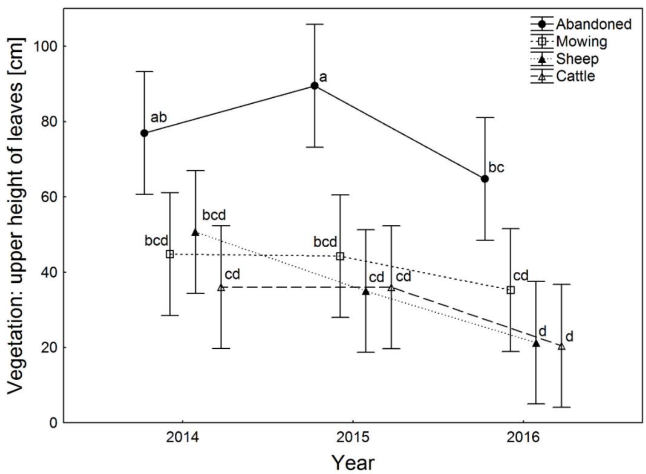

Figure A. 1. The average height of the upper height of leaves the vegetation of survey plots. Whiskers denote 95% confidence interval of means. Letter-labels denote homogeneity groups according to the Tukey multiple comparison test, performed as post-hoc test after mixed-model tests (Table A.2).

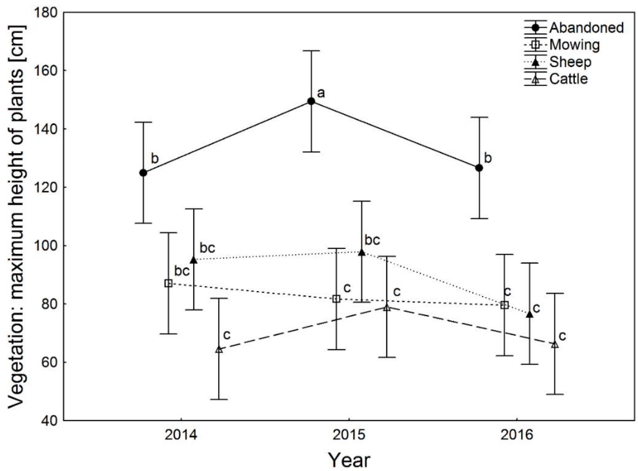

Figure A. 2. The maximum height of vegetation in plots by year. Whiskers denote 95% confidence interval of means. Letter-labels denote homogeneity groups according to the Tukey multiple comparison test, performed as post-hoc test after mixed-model tests (Table A.2).

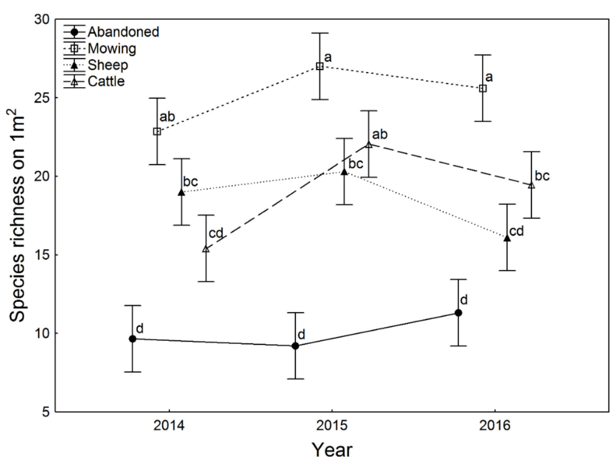

Figure A. 3. The species richness in plots by year. Whiskers denote 95% confidence interval of means. Letter-labels denote homogeneity groups according to the Tukey multiple comparison test, performed as post-hoc test after mixed-model tests (Table A.2).

Table A. 3. The results of the mixed model about proportional distribution of one-leaved (juveniles) and two-leaved (premature) plants by bulb morphology.

	Bulb-leaf distribution		
Effect	df	F-statistic	P
Treatment	3;4	0.77	0.5698
Stage	3;12	10.12	0.0013
Treatment*Stage	9;12	4.63	0.0081
Covariance parameters	Estimate	Z-statistic	P
Random: SubSite(Treatment)	-0.012	-1.87	0.0608
Residual	0.061	2.45	0.0072

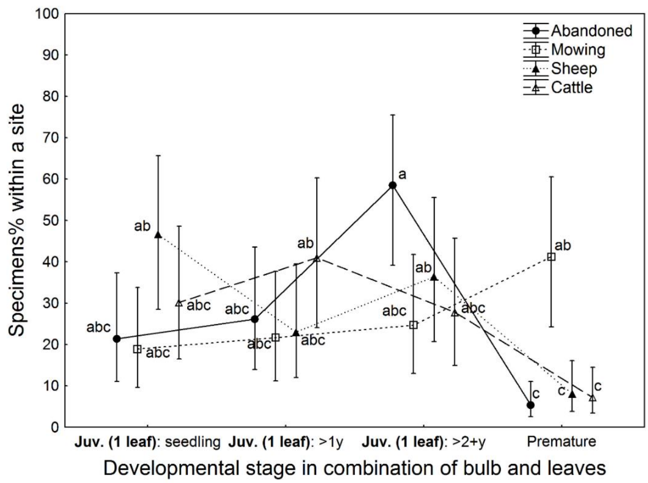

Figure A.4. The proportion of one-leaved (juveniles) and two-leaved (premature) plants by bulb size and morphology. Whiskers denote 95% confidence interval of means. Letter-labels denote homogeneity groups according to the Tukey multiple comparison test, performed as post-hoc test after mixed-model tests (Table A.3)

Table A. 4. The test results of mixed model about differences in the proportion of browsed plants of *G. imbricatus* among stages by year and treatment.

Effect	Proportion of browsed plants 2014-2016 df	F-statistic	P
Treatment	1;16	2.59	0.1273
Stage	2;16	26.47	<0.0001
Treatment*Stage	2;16	7.50	0.0050
Year	2;16	0.24	0.7884
Treatment*Year	2;16	13.77	0.0003
Stage*Year	4;16	0.10	0.9801
Treatme*Stage*Year	4;16	3.03	0.0487
Covariance parameters	Estimate	Z-statistic	P
Random: SubSite(Treatment)	0.041	0.64	0.2596
Repeated: Stage(Subsite) by Year	-0.073	-1.04	0.3001
Residual	0.405	2.45	0.0072

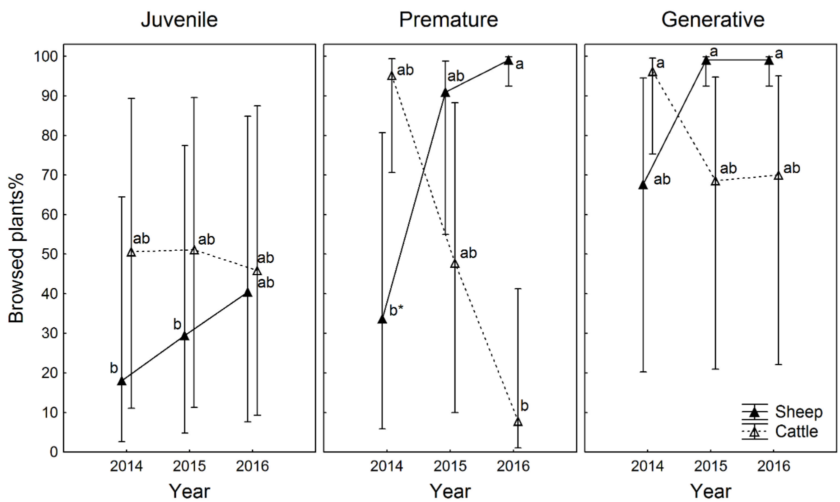

Figure A. 5. The leaf-browsing proportions of *G. imbricatus* specimens across stages in three years. Whiskers denote 95% confidence interval of means. Letter-labels denote homogeneity groups according to the Tukey multiple comparison test, performed as post-hoc test after mixed-model tests (Table A.4).

III

Moora, M., Kose, M., Jõgar, Ü. 2007. Optimal management of the rare *Gladiolus imbricatus* in Estonian coastal meadows indicated by its population structure. Applied Vegetation Science, 10, 161–168.

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Optimal management of the rare *Gladiolus imbricatus* in Estonian coastal meadows indicated by its population structure

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Abstract
Questions: What is the best grassland management regime for the threatened plant species *Gladiolus imbricatus*; is the stage structure of local populations a feasible indicator of the effect of changed management.
Location: Coastal meadow system in southwestern Estonia.
Methods: The effect of five management regimes was studied in a long-term (three-year) field experiment: (1) mowing in late July, (2) grazing by cattle, (3) grazing by sheep, (4) sheep grazing during the first year and mowing during subsequent years, (5) no management (control).
Results: The population density increased significantly in response to the mowing treatment and to the mowing after sheep grazing treatment. The proportion of grazed plant individuals was higher in the sheep-grazed than in the cattle-grazed treatment. Generative and vegetative adult individuals of *G. imbricatus* were significantly more damaged by cattle herbivory than juveniles. All management regimes shifted the population structure towards a dynamic state where juvenile stages dominate, while the not managed control retained a regressive population structure.
Conclusions: Population stage structure was a useful indicator of different management conditions, even in the case where population density did not differ. As indicated by population stage structure, the best management regime for *G. imbricatus* was either mowing in late July only, or alternation of grazing and mowing in different years.

Keywords: Grassland management; Grazing; Life-Nature programme; Mowing; Population dynamics; Restoration.

Nomenclature: Tutin et al. (1972 a.f.).

Introduction

The development and persistence of the species-rich semi-natural grasslands in Europe is associated with a long history of traditional management – the grazing of domestic animals and haymaking over hundreds of years (Kull & Zobel 1991; Eriksson et al. 2002). Due to the abandonment of traditional farming during the 20th century, the number and size of semi-natural grasslands have dramatically declined in Europe (Willems 2001). Plants in semi-natural grassland communities are therefore faced with habitat loss, population fragmentation and isolation, resulting in the extinction of local populations (Harrison & Bruna 1999).

During recent decades, semi-natural grasslands have been recognized as important targets in conservation due to their species-rich flora and fauna and due to their cultural value as part of traditional landscapes (WallisDeVries et al. 2002). The persistence of many plant species in semi-natural grasslands depends on regular and appropriate management. Consequently there is a need to understand how threatened plant species respond to different management conditions.

Individual-level experimental manipulations with rare species may give us important information about the potential significance of different environmental factors (Eckstein & Donath 2005) or ecological interactions (Moora et al. 2004; Rünk et al. 2004; Moora & Jõgar 2005) behind their rarity, but the real performance of rare plant species populations in nature can only be addressed through large scale experimental manipulations and/or the restoration of the resident communities.

Populations may respond slowly to habitat deterioration, and the current size or density of populations may not indicate the potential of a population to change in the future (Helm et al. 2006). The population structure, indicating the current demographic status of a population, may offer a much better basis to make predictions for the future (Rabotnov 1985). The use of population structure in characterizing population status has proven to be successful in a number of studies of perennial plant species, including rare and endangered species (Oostermeijer et al. 1994; Bühler & Schmid 2001; Hegland et al. 2001; Aguraiuja et al. 2004; Eckstein et al. 2004; Endels et al. 2004).

Population structure may be described by classifying the individual plants by age, size or life stage (Gatsuk et al. 1980). On the basis of population stage structure, one may identify three main types of population (Rabotnov 1985) (1) dynamic populations, characterized by a large proportion of early ontogenetic life stages; (2) stable populations with a varying proportion of all life stages; (3) regressive populations with predominating later ontogenetic life stages. Regressive populations are currently of great concern in plant conservation (Aguraiuja et al. 2004), since habitat destruction and fragmentation lead to extinctions of local populations, and the existence of a regressive population may be partly responsible for extinction debt (Helm et al. 2006), i.e. indicate the delayed response of perennial plants to unfavourable conditions.

Coastal meadows are common seashore communities along the extensive coastline of Estonia. These open landscapes are preserved due to floods, grazing (by migratory water birds and livestock) and mowing (Jutila 2001). In particular, grazing management was preferred near the shoreline and in stony areas, while areas at higher elevations and with fewer stones were mowed in midsummer and grazed later. Coastal meadows are habitats for several rare plant species; *Gladiolus imbricatus* is one of the most spectacular species. Without management, overgrowing succession will start, and many plant and animal species characteristic of coastal meadows may disappear within 10 to 20 years (Leibak & Lutsar 1996). We focused on *G. imbricatus* as a model species to test the effect of different grassland management on population stage structure, in order to suggest the optimal management regime. *G. imbricatus* is red-listed in Estonia (Lilleleht 1998), and is also a decreasing species in Europe (Schnittler & Günther 1999).

In particular, we hypothesised that population stage structure is a valuable indicator of changed management conditions in coastal semi-natural grasslands. We addressed the effect of five different management regimes (cattle grazing, sheep grazing, mowing, one-year sheep grazing followed by two-year mowing, and no management) during the three-year field experiment.

Material and Methods

Study species

Gladiolus imbricatus (*Iridaceae*) is native to Central and Eastern Europe, the Mediterranean, Caucasia and West Siberia (Tutin et al. 1972). *G. imbricatus* grows in coastal and flooded, but also in mesophytic, meadows and marshes. In Estonia the number of local populations has decreased due to the cessation of grassland management and currently only a few local populations are known (Kukk & Kull 2005).

G. imbricatus is a 40 to 60 (100) cm-high perennial plant with tubers of 1 to 2 cm diameter. Flowering in Estonia in July, the seeds mature from the end of July to the first half of August, and germinate the following spring. Vegetative spread is limited, and production of more than one daughter corm within one season is rare (Klimeš et al. 1997). Reproduction from seeds is common (Jõgar & Moora pers. obs.).

Study site

The coastal meadows of Häädemeeste (the area of the meadows is ca. 800 ha) belong to the Rannametsa - Soometsa Nature Reserve on the southwestern coast of Estonia. The meadows of this area are representative of the Boreal Coastal Meadow (1630, Natura 2000), a priority community type in the EU Habitat Directive (92/43/EEC). The meadows of Häädemeeste are a resident community for more than 250 vascular plant species. The height of the herb layer ranged from 5 cm in the sheep pasture to 50 cm in the non-managed meadow and in the mown meadow at the moment of sampling (data not shown). The meadow areas are edaphically homogeneous: a humus layer of ca. 15-20 cm is underlain by sandy loam. The community is species-rich (up to 35 vascular plant species per m^2, data not provided) and the dominant plant species are *Sesleria caerulea, Deschampsia caespitosa, Achillea millefolium,* and *Centaurea jacea*. *G. imbricatus* is a frequent subordinate plant species in this community, with a large population (more than 10 000 individuals) growing almost all over the suitable habitats in the Häädemeeste coastal meadow system.

In 2001, the EU LIFE-Nature programme project was launched in this reserve. The aim of the project was to preserve and restore objects of natural value, and to apply the most efficient management conditions for the preservation and enhancement of rare plant and animal species. Until 2001, most of the coastal meadow of Häädemeeste had not been managed for 10 years. One of the goals of the Life project was to recommence management by supporting the purchase of livestock and machinery by landowners. Sheep and cattle herds were purchased and pastures (fences) established in the autumn of 2001 and the spring of 2002. Mowing was also recommenced in either August 2001 or 2002.

Experimental design and sampling

In collaboration with landowners, management regimes were designed in order to satisfy the needs of a field experiment. In experiment A, four different management regimes were started in an edaphically uniform coastal meadow system, each in two separate plots (the minimal distance between the plots was 0.8 km and maximum 10 km) over the three seasons: (1) mowing after the flowering and seed ripening of *G. imbricatus* (Late July), (2) cattle grazing, (3) sheep grazing and (4) no management. The size of the treated plots was variable: cattle pastures occupied an area of 18 and 23 ha, sheep pastures 11 and 9 ha, meadows 20 and 2 ha and not managed plots 15 ha each, and grazing pressure was kept constant at one livestock unit (i.e. five sheep or one heifer) per ha. Due to the change in management regime as a result of one landowner's desire in one plot of land (6 ha), a fifth management regime – sheep grazing in the first year and mowing in the two following years – was included (Experiment B).

Within the above-mentioned management treatments, two randomly-selected 20 m × 20 m subplots (sampling areas) were established within each treatment type in June 2002. In the plot of land with the fifth management regime, one 20 by 20 m randomly selected subplot was established in 2002. There were a total of 9 subplots. Within each 20-m^2 subplot, ten 1-m^2 quadrates were randomly located annually in the first half of July (2002 to 2004) for the description of the local population of *G. imbricatus*. We did this annual random selection of quadrats inside the permanent subplot for two reasons: 1. The establishment and maintenance of permanent quadrats in the harsh environment of the coastal meadow would be very problematic in a large scale experiment. 2. A random selection procedure is an appropriate way to obtain a more independent sample of population structure in different years. Both complete and grazed individuals of *G. imbricatus*, representing one of three life stages, were carefully counted in each quadrate. We distinguished between juvenile, mature vegetative and generative life stage. All individuals with only one leaf were classified as juveniles. In order to avoid the disturbance of local populations due to uprooting, we did not distinguish seedlings and young vegetative individuals originating from a daughter corm. Vegetative individuals had more than one leaf. All individuals with a stem that was flowering at the moment of sampling were classified as generative.

Statistical analysis

All statistical tests presented here were performed on data from the first and last season of the experiment – 2002 and 2004. We used the Statistica 6.0 software package (Anon. 2001).

The numbers of individuals (total, juvenile, vegetative, generative) of *Gladiolus* and the relative number of grazed individuals (grazed individuals/total individuals, hereafter grazing proportion) were analysed using ANOVA, where a two-level factor 'subplot' was nested within the four-level factor 'management', while sampling year was considered as a two-level factor. The data from Experiment B was analysed separately with one-way ANOVAs, where year with two levels was used as a factor. Variables were log-transformed to meet the assumptions of the analysis. In order to estimate the differences between the treatments, the Tukey HSD post hoc multiple comparison test was applied with a significance level of 0.05.

In order to compare the response of the structure of experimental populations to the recommenced management, the χ^2-test and Freeman-Tukey deviation test (FTD test) (Legendre & Legendre 1998) were used to compare the empirical frequencies of individuals in different developmental stages with that predicted by the null model, representing frequencies from the first year of observation, when the experimental manipulations had just been started (Table 1).

Log-linear analysis and the FTD test (Legendre & Legendre 1998) were used to estimate the effect of sheep and cattle grazing on the frequency of browsed individuals in different developmental stages. Year, management, developmental stage and grazing proportion (grazed, non-grazed) were the factors used in the analysis.

Results

Changes in abundance of *Gladiolus imbricatus*

Experiment A. Main experiment

Different management regimes had a significant main effect on the total density of *G. imbricatus* (Table 2) – the highest density was recorded in the mown plots. There was a significant interaction between year and management (Table 1, Table 2, Fig. 1) – there were no changes in the density of *G. imbricatus* in grazing treatments, while density increased in the control and mowing treatments during the experiment. The increase was significantly higher in the mowing treatment compared to the control treatment (Fig. 1).

The number of juvenile individuals increased significantly during the experiment (Table 2, Fig. 2A). The

Table 1. Life stage structure and total number of individuals in experimental populations from 2 × 20 m^2 (20 m^2 in treatment 5*) at the beginning and the end of the management experiment. According to the χ^2 and Freeman-Tukey deviation test, statistically significant (P < 0. 05) increases (^{incr}) and decreases (^{decr}) in stage proportion between the years inside the treatment are indicated. Expected proportions are always calculated based on the proportions in the first sampling year (2002).

Treatment	Proportion of life stage 2002				Proportion of life stage 2004			
	Juvenile stage	Vegetative stage	Generative stage	Number	Juvenile stage	Vegetative stage	Generative stage	Number
No management	0.518	0.181	0.301	166	0.787	0.075	0.138	507
Mowing	0.498	0.144	0.358	492	0.842 ^{incr}	0.078	0.080 ^{decr}	2220
Sheep grazing	0.408	0.223	0.369	358	0.930	0.050	0.020 ^{decr}	343
Cattle grazing	0.493	0.219	0.288	292	0.931	0.043	0.029 ^{decr}	435
Sheep grazing/ mowing*	0.408	0.223	0.369	214	0.819 ^{incr}	0.066 ^{decr}	0.115 ^{decr}	1913

increase was evident in all treatments except the sheep grazing treatment (Fig. 2A). The number of vegetative individuals decreased significantly during the experiment (Table 2, Fig. 2B). There were differences between experimental treatments: the number of vegetative individuals did not change in the control, increased in the mowing treatment, decreased significantly in the sheep pasture and marginally non-significantly (P = 0.08, Tukey HSD test) in the cattle pasture.

The number of generative individuals decreased during the experiment (Table 2, Fig. 2C). The number of generative individuals did not change in the case of the control and mowing treatment. During the experiment, both grazing treatments decreased the number of generative individuals significantly (Fig. 2 C).

Experiment B. Former sheep pasture

There was a significant increase in the number of *Gladiolus* individuals during the experiment (Table 1):

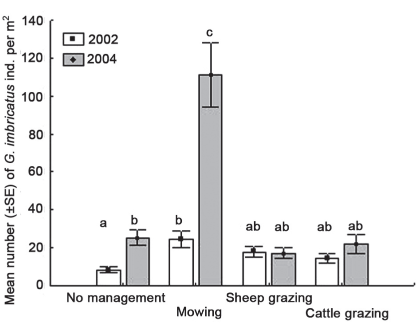

Fig. 1. Mean total number of individuals of *Gladiolus imbricatus* in 1-m^2 plots in the coastal meadow of Häädemeeste at the beginning of the experiment (2002) and the end of the experiment (2004). Bars with different letters are significantly different (P < 0.05) according to the Tukey HSD test.

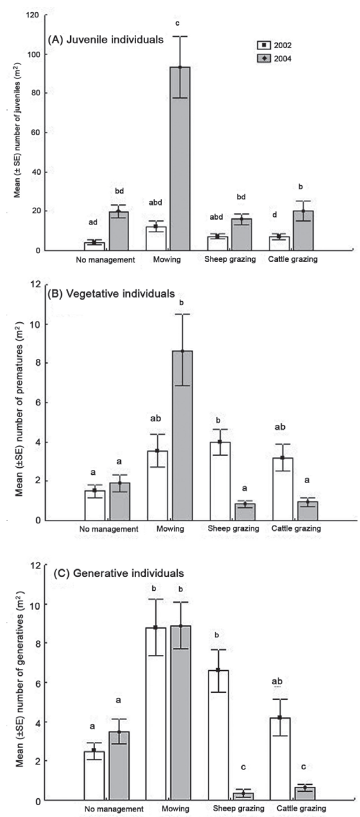

Fig. 2. The response of the different life stages in local populations of *Gladiolus imbricatus* in the coastal meadow of Häädemeeste to the four different management regimes in the years 2002 and 2004. Bars with different letters are significantly different (P < 0.05) according to the Tukey HSD test.

Table 2. Results of ANOVAs – the effect of different experimental management treatments (management), sampling time (year) and their interaction on the mean total density (per 1 m^2), mean density of different life stages of *Gladiolus imbricatus* and on the mean proportion of grazed individuals.

Source of variation	*df*	Total number			Juvenile number			Premature number			Generative number			Grazing proportion			
		MS	*F*	*P*	*MS*	*F*	*P*	*MS*	*F*	*P*	*MS*	*F*	*P*	*df*	*MS*	*F*	*P*
Management	3	9.560	10.52	0.000	820.18	789.46	0.000	3.50	7.75	0.000	8.85	17.41	0.000	1	0.827	30.5	0.000
Year	1	13.13	14.44	0.000	52.11	50.16	0.000	2.87	6.35	0.013	25.80	50.76	0.000	1	0.004	0.14	0.706
Subplot (management)	4	1.725	1.9	0.114	1.26	1.21	0.309	2.74	6.07	0.000	1.42	2.79	0.029	2	0.291	10.73	0.000
Management * Year	3	2.993	3.29	0.022	2.44	2.35	0.075	3.74	8.29	0.000	4.01	7.89	0.000	1	0.176	6.48	0.013
Error	148	0.909			1.04			0.45			0.51			69	0.027		

total no. of individuals ($F_{df=1,18} = 36.3$, $P < 0.001$),
no. of juvenile individuals ($F_{df=1,18} = 71.6$, $P < 0.001$),
no. of vegetative individuals ($F_{df=1,18} = 4.7$, $P < 0.044$),
no. of generative individuals ($F_{df=1,18} = 8.9$, $P < 0.008$)

Changes in Gladiolus imbricatus population stage structure

The analysis of population structure showed that experimental management treatments changed the structure differently during the experiment ($\chi^2 = 3272.7$, $P < 0.001$, $df = 14$) (Table 1). In the control treatment, the population structure remained unchanged, while all manipulated populations responded to the management. Mowing treatment resulted in a significantly higher proportion of juvenile plants and lower proportion of the generative plants than anticipated by the null-model (Table 1). In both grazing treatments, proportions of generative plants were significantly lower than anticipated by the null-model (Table 1). In experiment B (sheep grazing followed by mowing), the proportion of juvenile plants was significantly higher, and the proportion of vegetative and generative plants lower than anticipated by the null-model (Table 1).

Grazing intensity

In non-grazed treatments, less than 3% of recorded *G. imbricatus* individuals were grazed (wild deer were observed in the site). Since our task was to estimate the effect of different intensities of livestock grazing on *G. imbricatus*, the data from non-grazed treatments were not considered in this analysis. There were significantly more (Table 2) grazed individuals in the sheep pasture than in the cattle pasture – 47 % and 28 % respectively. Grazing intensity did not differ over the years. The interaction between the year and management regime was significant, since the grazing intensity of the sheep was similar over the years, while the grazing intensity of the cattle on *Gladiolus* decreased in the last year of the experiment.

The best initial model of log-linear analysis involved all three-way interactions (Pearson χ^2 of the goodness of fit of the final model: $\chi^2 = 1.52$, $df = 2$, $P = 0.467$). Life stages were characterised by significantly different grazing proportions ($\chi^2 = 145.76$, $df = 2$, $P < 0.001$): 27 % of juvenile, 62% of vegetative and 85% of generative individuals were grazed. Significant interaction between year and life stage and grazing proportion ($\chi^2 = 10.86$, $df = 2$, $P < 0.005$) became evident – there were no differences in grazing proportion between life stages in 2002, but in 2004 the individuals in the vegetative and generative life stage were more grazed than anticipated by the null model ($P < 0.05$, FTD test). There was a significant interaction between management, life stage and grazing proportion ($\chi^2 = 8.03$, $df = 2$, $P < 0.02$) – the vegetative individuals in the sheep pasture were less grazed, and vegetative and generative individuals in the cattle pasture were significantly more grazed ($P < 0.05$, FTD test) than expected by the null model.

Discussion

The results of the field experiment show that particular management regimes may have different impacts on the density and demographic structure, and thus also on the viability of the local populations of a rare plant species. All local populations of *Gladiolus imbricatus* had a relatively similar life stage structure at the beginning of the experiment – the share of juvenile and generative stages was higher than that of the vegetative adult stage. When lumped together, vegetative and generative stages made up a similar proportion to the juvenile stage. Though the stage structure of the ideal equilibrium population of *G. imbricatus* is unknown, a strong response to the recommenced management (significant increase in the juvenile proportion) gives reason to assume that local populations of *G. imbricatus* in the coastal meadows of Häädemeeste might have been regressive at the beginning of the field experiment. All management types increased the share of the juvenile stage, while in the control, this increase remained non-significant. Evidently the resumption of management shifted the population type from regressive to dynamic. Thus as in other grassland species (e.g. Moora et al. 2003), the removal of plant biomass via grassland management enhanced the establishment of young individuals of *G. imbricatus*. The strong positive response of the juvenile stage to management indicates that in the community under investigation, *G. imbricatus* is microsite rather than diaspore limited, and a proper management regime is needed for the restoration and conservation of viable local populations.

Although there is mixed evidence of whether grazing or mowing results in higher species richness in semi-natural grasslands (Kull & Zobel 1991; Hansson & Fogelvors 2000), population-level studies of grassland perennials have indicated that mowing after the flowering period, compared to grazing or mowing too early, may favour populations (Hegland et al. 2001; Brys et al. 2004). In the coastal meadows of Häädemeeste, mowing was clearly the most favourable management regime for *G. imbricatus* – a significant increase in the density of populations in mown areas, compared to other management regimes, became evident. The increase in population density was mainly due to the increased numbers of the juvenile and vegetative individuals, but also due to the stable number of generative individuals. A similar trend was observed in a former sheep pasture, in experiment B.

There was a slight increase in the number of juvenile plants in the cattle pasture, associated with the strong decrease in the numbers of the vegetative and generative individuals. Since sheep tend to graze turf lower than cattle (Grant et al. 1996), 7-8 cm high juveniles were evidently more likely to escape from the herbivory in the case of cattle than in sheep grazing management.

Although the average density of *G. imbricatus* did not increase in grazing treatments, the population stage structure shifted towards a more dynamic state due to an increased share of juveniles. This response may be due to both enhanced seed dispersal and better establishment conditions in grazed and trampled vegetation. The positive effects of grazing on the establishment of *G. imbricatus* did not result in increased total population density, since the sheep and cattle damaged the generative and vegetative individuals significantly more than juveniles. Since the number of generative individuals was low anyway, and many of them were browsed, there may be almost no seed production in a local population of grazed areas due to the damage of generative stages of plants by browsing, and trampling may result in the deterioration of population structure due to increasing seed limitation (Lennartsson & Oostermeijer 2001). According to the traits reviewed by Díaz et al. (2001), *G. imbricatus* is expected to be a grazing-susceptible species – it is high, with relatively large, hard leaves and has limited vegetative spread. Thus continuing grazing pressure may lead to a decrease in local populations, despite the fact that stage structure resembles that of a dynamic population.

Most certainly, management either via mowing or grazing prevents grasslands from overgrowing with woody plants and *Phragmites australis* (i.e. Rosén & Bakker 2005). Also, both haymaking machinery (Strykstra et al. 1997) and grazing animals (Fischer et al. 1996) are important seed vectors. At the same time, the mowing treatment resulted in the highest absolute densities of *G. imbricatus*, as well as the highest share of the juvenile stage in local populations. The structure of local populations in the 'former sheep pasture' treatment showed that the replacement of sheep grazing by mowing shifted the population towards a dynamic state. Since mowing took place after the seeds of *G. imbricatus* ripen and after hay was dried in the meadow, one may expect no seed limitation due to management (Svensson & Carlsson 2005). At the same time, early sheep grazing may result in severe seed limitation of meadow species, while the number of seedlings increased in meadows that were grazed later (Brys et al. 2004). Thus, avoiding grazing or shifting the time of grazing may have a tremendous effect on local populations.

Conclusions for restoration practice

When searching for the best management regime for *G. imbricatus* in the coastal meadow of Häädemeeste, one may argue in favour of mowing in late July. At the same time, such a management regime may be incompatible with other targets of grassland management. Mowing of the shoreline is almost impossible with machinery and very inefficient by hand, but it is very important that the shoreline of coastal meadows be kept open for nesting birds such as the Dunlin, Black-tailed godwit, Redshank and Ruff. These are the most rapidly declining coastal meadow birds in Estonia and throughout Europe (Thorup 2004). Grasslands support several plant and animal species that may benefit from different management regimes (Hulme et al. 1999; Stammel et al. 2003). In addition, local farmers do not need hay in large quantities, since grazing animals spend most of their time in the meadow. Grazing will certainly remain the most efficient and cheapest management tool to prevent the overgrowing of semi-natural coastal meadows.

In a coastal meadow system such as Häädemeeste, we suggest the use of alternate management regimes where cutting and grazing are both used alternately in the same fields in different years. If mowing is not possible, some areas may be closed for grazing during the first half of the vegetation period. Such a patchy management scheme will provide suitable conditions for seed production and for the establishment of new individuals of *G. imbricatus*, as well as for other plant species potentially susceptible to grazing.

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